THE JOURNAL
OF
COMPARATIVE AND
PHYSIOLOGICAL PSYCHOLOGY

478Z2

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VOLUME 47, 1954

American Psychological Association, Inc.

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SPECTRAL SENSITIVITY OF THE TURTLE, *PSEUDEMYS*

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Many questions regarding the visual behavior of the turtle remain unanswered. The present paper is concerned primarily with two, namely its spectral sensitivity and the possibility of a functional night-vision mechanism.

The chelonian retina has long been regarded as capable of functioning only under photopic conditions, a belief which is based largely upon early anatomical observations. More recently, a few investigators (7, 14, 15) have claimed that it possesses occasional scotopic receptors. There has been no demonstration, however, that these extremely sparse units are of any importance in the animal's behavior (6).

A different approach may be made through a study of the electroretinogram (ERG) and its component waves. Evidence concerning sensitivity to stimuli of different intensity and varying wave lengths has been obtained, and records have been examined for scotopic potentials. In addition, the electrophysiological findings have been related to a behavioral determination of dark-adapted relative spectral sensitivity.

METHOD

Apparatus

Electrical recording apparatus used for recording the ERG was essentially the same as has been used with the human eye (10, 13), the only important modification being the addition of supports for an animal preparation. Accordingly, its operation will only be outlined here. There were two basic pieces of equipment: One delivered flashes of known spectral composition and intensity to the eye, and the other recorded electrical responses.

Stimulator. The stimulator consisted of an array of lenses, optical filters, a 50 c.p. tungsten lamp, and a shutter, all of which were rigidly mounted so as to present a uniform circular stimulus patch subtending an angle of 7.5° at the pupil. Intensity and spectral composition were varied with interchangeable, neutral density filters calibrated so that the relative amounts of energy contained in successive stimulus flashes were known (2). Stimuli had a duration of 0.02 sec.

Recorder. For recording, a pair of conventional cotton wick electrodes, one placed upon the cornea and the other inserted into the mouth, were used. Signals from the electrodes were led to both a direct-coupled and a capacitance-coupled amplifier. The capacitative channel (from which we have taken most of our measurements) permitted stable recording with a high gain. The direct-coupled tracing was examined to be certain that the capacitative system was faithfully reproducing the principal features of the electroretinogram. In addition, a time scale and a signal mark indicating the occurrence of a test flash appeared on the photographic record.

Apparatus for behavioral observations. A modified Yerkes discrimination box consisting of a rectangular tub or runway filled with 6 in. of water was used to determine relative spectral sensitivity on the basis of performance (Fig. 1). The animal was required to move from the starting box at one end to either of two alleys at the other end. A lighted stimulus screen at the end of the "correct" alley indicated the proper choice. As a reward, a bit of horse meat supported by a small hook could be lowered immediately in front of the lighted panel.

The stimulus screens were panels of opal glass upon which light was projected from the monochromator section of a Beckman D. U. spectrophotometer. This was accomplished by means of a system of achromatic lenses and mirrors which produced a 1-in. by ¾-in. image of a stop actually located within the spectrophotometer. The apparatus was calibrated so that the relative energy transmitted at each wave length and intensity was known to *E*. Stimulus intensity was controlled with neutral density filters. A tungsten filament maintained at a temperature of 2,700° K served as a light source.

As the apparatus was kept in complete darkness, *E* could not observe the animal directly. To overcome this difficulty, a signal system was employed. Whenever a turtle entered an alley, it pushed aside a lever or gate, which in turn closed a switch activating a pilot lamp circuit. Light from this lamp was not visible from the runway.

Procedure

Electrical recording. A procedure which allowed repeated use of the same animals was adopted. At the beginning of an experimental session, a turtle was injected with approximately 8 mg. of d-tubocurarine chloride per kilogram of body weight. The action of the drug is gradual; even though no immediate effect was noticeable, complete paralysis set in 30 to 40 min. later. The animal was then attached to the stimulator. To permit breathing, a cannula connected with a mechanical respirator was inserted through the mouth into the glottis. Finally, the electrodes were adjusted and alignment was made with the optical system. Al-

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[1] These experiments were performed at Brown University under support of the Office of Naval Research, Department of the Navy. The author would like to express his gratitude to Professor L. A. Riggs for advice and suggestions made in regard to this work.

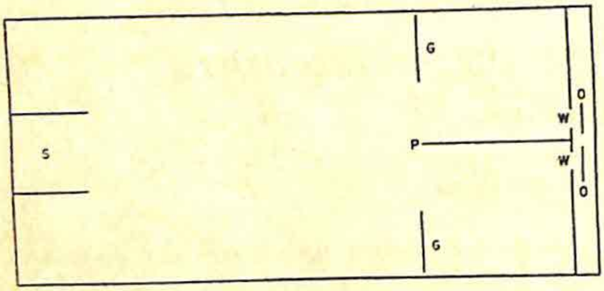

FIG. 1. Floor plan of the runway apparatus

S, starting box; *G*, hinged signal levers or gates; *P*, dividing partition separating runway into two alleys; *W*, windows; *O*, opal glass screens. To secure the reward, the animal had to thrust its head through a window, *W*, and bite at food which was suspended from a hook immediately in front of *O*. The window guided the animal's head to the proper place for feeding. The runway measured 5 ft. by 2 ft.

though this completed initial preparations, actual recording did not begin until there had been at least 45 min. of dark adaptation.

Test flashes were administered at 2-min. intervals, and recording was carried on for 2 or 3 hr. Upon termination of the experimental session, the turtle was injected with sufficient neostigmine methyl-sulphate solution to counteract curare and relieve paralysis.

All recording was performed at a room temperature of 25° ± 3° C.

Measurement of records. It is evident from the records shown in Figure 2 that the electrical response consists of several successive waves. Experiments were performed to provide information concerning (*a*) the relationship between height of each of these responses and stimulus intensity, (*b*) the relation between latency and stimulus intensity, and (*c*) relative spectral sensitivity. Controls were performed (*a*) to see what effect, if any, curare has upon the electroretinogram, (*b*) to see whether deterioration of the ERG takes place during an experimental session, and (*c*) to see whether an "off effect" may account for any of the waves.

Measurements of amplitude and delay have been made as follows: Amplitude of the entire response is measured from its most negative to its most positive point; amplitudes of individual waves are measured from negative troughs to the positive crests immediately following, and delay or implicit time is measured from the onset of the stimulus to individual positive crests.

The main steps required for computation of relative spectral sensitivity are as follows: A plot is made of the magnitude of the activity in question as a function of stimulus intensity. The degree of neutral filtering necessary to decrease response to a criterion magnitude is read from the plot. Since the energy emitted by the source and transmitted through the color filters is known,[2] it is possible to reduce this value by the amount of neutral filtering and hence to determine the energy demanded for the criterion. Measures of this sort made with each spectral filter provide an indication of spectral sensitivity. A criterion height of 25 microvolts was used to investigate relative spectral sensitivity of the entire response; 12 microvolts were used for individual waves.

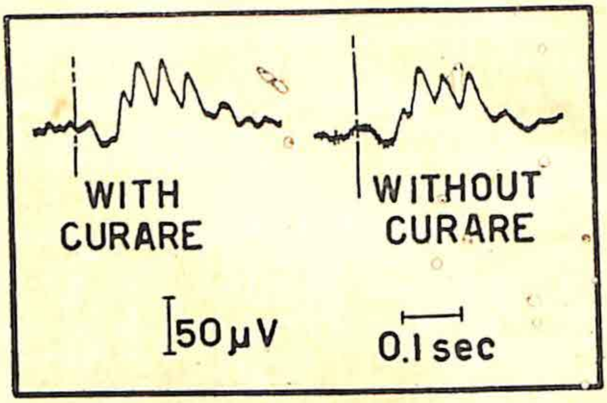

FIG. 2. Typical turtle electroretinograms. Stimulus was white, 2.0 log units below maximum intensity, 0.02 sec. in duration. (Turtle 8)

Discrimination procedure. It was first necessary to train the animal to enter the alley with the illuminated panel. The reward was placed immediately in front of the stimulus area as the alley was entered. No punishment was administered for an incorrect choice. For early training very bright stimuli were used. As performance improved, the light was gradually reduced until the reward was no longer clearly visible. At this point the animal was forced to snap blindly at the lighted area until its mouth contacted the reward more or less by chance. Indeed, the lights were so weak that *E* was unable to see the animal. However, snapping movements were clearly audible, and when *S* finally bit the reward, it gave the supporting hook a vigorous tug. This signaled *E* that the reward had been obtained, and the turtle was returned to the starting box.

Well over three hundred training trials were required before the animal barely succeeded in making correct choices nine times out of ten with stimuli well above threshold. Then it was presented with a series of 375 stimuli of selected wave length and intensity. The entire procedure was extremely time-consuming. No more than 25 runs could be made per day. As a general rule, the animal required 2 to 3 min. to move the length of the runway. Occasionally it took still longer. If it delayed for more than 5 min., the trial was counted as a failure.

These experiments were performed after 19 hr. of complete dark adaptation. The temperature of the water in the runway was kept at approximately 25° C.

Subjects

Turtles used in these experiments may be classified as *Pseudemys scripta elegans* (5). The spectral data for the ERG are based on results from three animals, those for performance on one.

RESULTS

Characteristics of the ERG. A typical electroretinogram consists of an initial negative deflection followed by a series of brief, sharp, positive waves, as shown in Figure 2. The particular form of the response cannot be attributed to use of the drug curare. As a control, a few responses were obtained without the administration of any drug, and these exhibited essentially the same characteristics. Amplitude of the complete response seldom exceeded 75 to 100 microvolts. Figure 3 shows responses to flashes having a duration of 15 sec. As the intensity of the stimulus increases, two effects may be seen: (*a*) the individual components become larger and (*b*) more waves are apparent. There is almost no "off" response except with the most intense stimulus. This demonstrates that the small positive waves or ripples are not a summation of an "on" and "off" response. In fact, when an "off" effect is present with appreciable magnitude, it too is superimposed with several small oscillations. The way in which response changes with stimulus intensity may be understood further by referring to Figure 4. Much could be said about these graphs. However, we wish to make three main points: (*a*) The height of each of the component waves increases more or less regularly with stimulus intensity. (*b*) The later waves are always smaller and tend to disappear with weaker stimuli. (*c*) Although changes in latency are less striking, there is a definite trend toward greater delay as the stimulus is weakened.

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[2] The original calculations of Riggs, Berry, and Wayner were available (13). They have been reworked to provide the necessary information.

The points on these plots represent individual measurements from a single animal. Thus, some idea of the degree of variability encountered in the present experimentation is provided. They are presented, not only because of the information they contain in themselves, but because they are typical of the intensity curves which were obtained with each color filter in the investigation of relative spectral sensitivity.

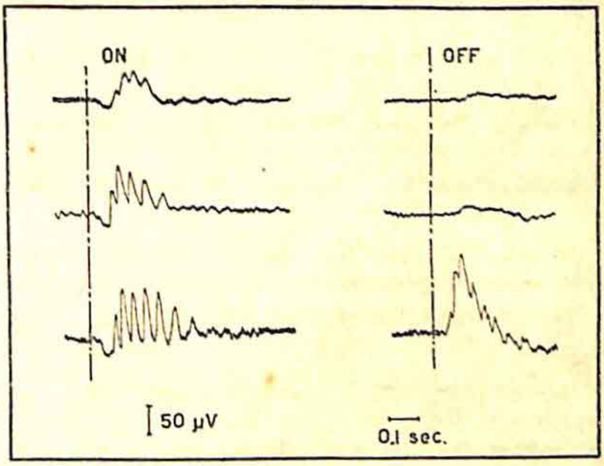

FIG. 3. "On" and "off" responses. From top to bottom, responses were obtained with a white stimulus, 2.0, 1.0, and 0.0 log units below maximum available stimulus intensity. A large "off effect" was seen only with the brightest stimuli. (Turtle 4)

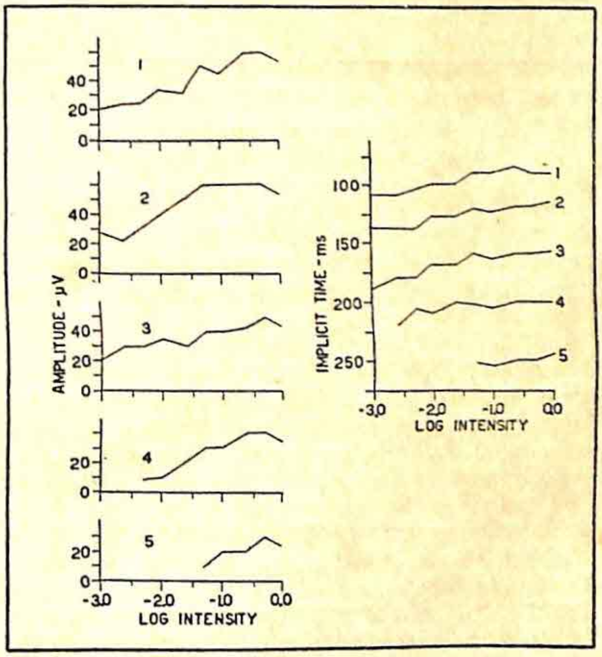

FIG. 4. Changes in height and latency of the first five waves as affected by stimulus intensity. Points are connected by straight lines. Each point represents a single measurement. White light was used as a stimulus. (Turtle 1)

Spectral sensitivity of the ERG. Response to selectively filtered stimuli is illustrated in Figure 5. Red light elicits potentials of appreciable magnitude which may be followed through a considerable intensity range. On the other hand, violet light is less effective. If we look for two responses of the same height, one of which is elicited by a short wave-length stimulus and the other by a longer wave-length stimulus, we find that ripples are more evident when a long wave-length stimulus is employed. This indicates that the electroretinogram of the turtle may have two underlying processes. One of these, resulting in a smooth, low-amplitude B wave is more sensitive to blue light, while the other, resulting in a series of marked positive potentials, is seen with greater magnitude when red stimuli are administered.

As a measure of relative spectral sensitivity, we have determined the relative amounts of energy required to elicit responses of criterion

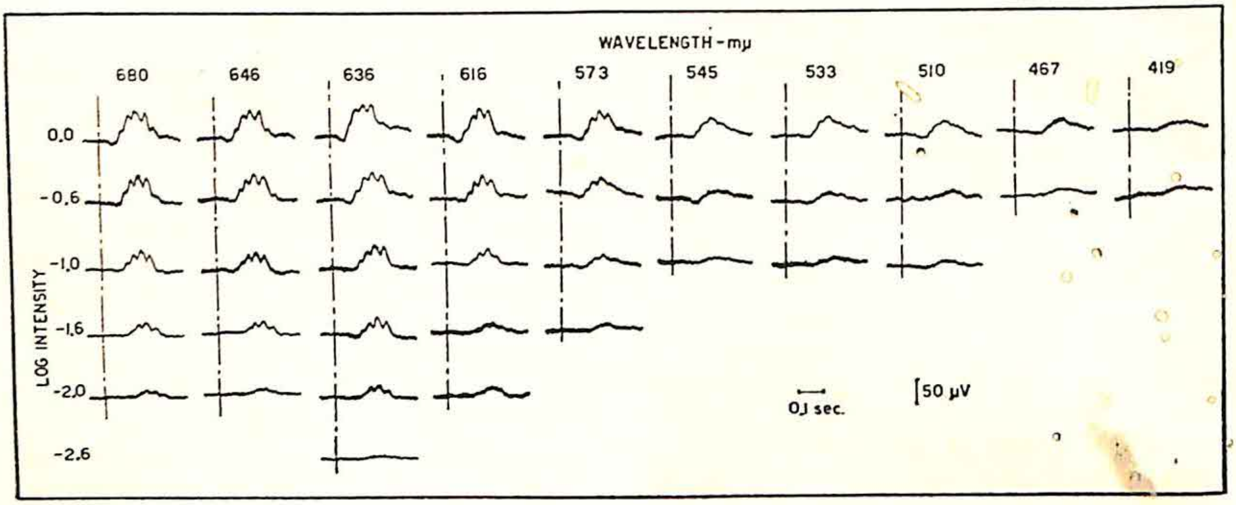

FIG. 5. Responses to stimuli of different wave length and intensity. Zero stimuli of different wave lengths do not necessarily possess equal visual effectiveness; the intensity scale merely refers to the degree of neutral filtering employed. The wave-length value assigned to each interference filter is that of its transmission peak. (Turtle 5)

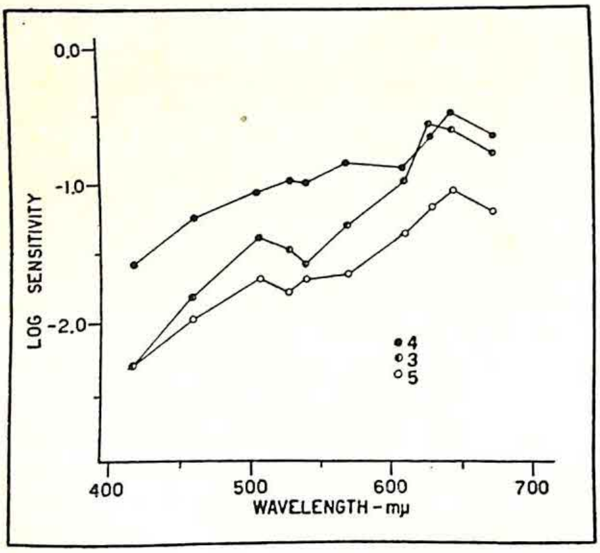

FIG. 6. Relative spectral sensitivity curves for three turtles. These curves are based on the height of the entire response.

amplitude. Such data, based on the total height of the response as measured from its most negative to its most positive point, are given in Figure 6. Each curve is based upon about one hundred stimuli. Vertical displacement of one curve from another is used to represent differences in absolute sensitivity. For example, the ERG of turtle 4 was roughly three-fourths of a log unit more sensitive throughout the

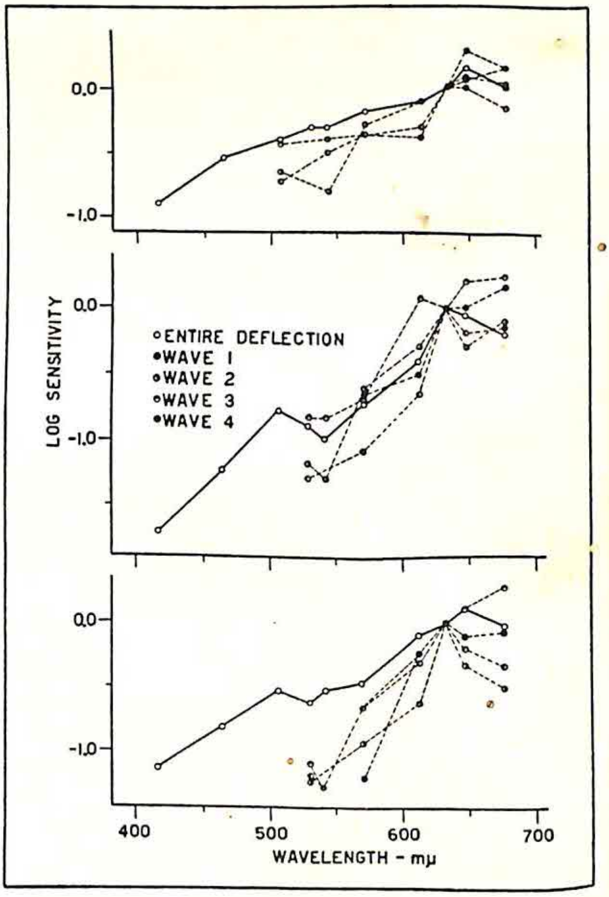

FIG. 7. Relative spectral sensitivity of the component waves of the ERG (turtles 4, 3, and 5)

spectrum than that of turtle 5, while turtle 3 was quite sensitive to red light and less sensitive to blue. The results are presented in this way to show the degree of variation from one preparation to another.

Spectral sensitivity of individual ripples may be found also, as shown in Figure 7. To facilitate comparison, all curves have been arbitrarily equated at 636 mμ. It is evident at once that the sensitivity of each of the individual waves is highly correlated with that of the others. Indeed, at the red end of the spectrum at least, sensitivity of the ripples is essentially the same as that of the height of the total response. No ripples of satisfactory magnitude for measurement were observed at the blue end of the spectrum.

Behavioral spectral sensitivity. The outcome of the behavioral studies is shown in Figure 8. A sensitivity curve having a maximum at about 525 mμ was obtained. A fact to be emphasized is that the turtle could successfully find extremely weak lights. All the stimuli used in these experiments were below the observer's color threshold no matter what the wave length. In fact, red stimuli which the turtle could find successfully were sometimes invisible to the human eye.

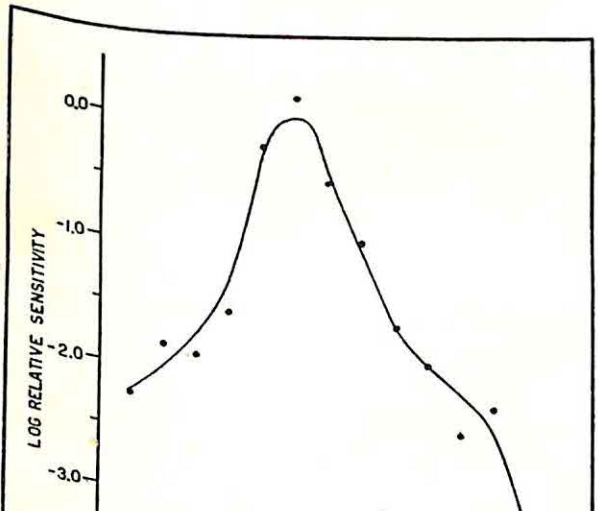

FIG. 8. Spectral sensitivity of a dark-adapted turtle (turtle 5) based upon performance in the runway

DISCUSSION

Form of the ERG. The positive, rippled electrical responses found in these experiments are quite similar in form to those found by Noell (11). They do not exhibit any such enormous negativity as that which has been observed by Bernhardt (4) and Granit (8, 9). It may be significant that their turtles, actually of a different species (12), were in the midst of hibernation and had been decapitated prior to recording. Adrian (2) has noticed an initial positive potential from the eyes of animals which possess photopic mechanisms. From studies of the human retina, it appears that the human photopic response too is characterized by one or more positive waves (1, 3).

Spectral sensitivity. The present electrical determination of spectral sensitivity is in agreement with that of Granit. At first glance the red maximum appears less prominent, but this is merely a result of our usage of logarithmic units of sensitivity. The unusual sensitivity of the turtle ERG to red stimuli may be related to the preponderance of receptors containing red oil droplets in this retina (14, 15). It has been conjectured that these act as selective wave-length filters, and may be used in color discrimination (4, 16).

Ripples. There has been no previous determination of the spectral performance of the individual ripples. They do not appear to be primarily concerned with color ability, as narrow bands of wave length will produce several fluctuations. One cannot say, for example, that the first wave is a manifestation of specific color activity, while the second is that of another, etc. Nevertheless, there is some support for the view that all these pointed waves are involved in response to the relatively long wave lengths. Only a comparatively low amplitude and smooth B wave could be elicited with blue and violet stimulation. The suggestion is that the turtle electroretinogram is a result of two complexes of activity. One of these, photopic in nature, gives rise to the prominent oscillatory ripples. The other, scotopic, produces a small, smooth B wave.

Comparison of spectral curves. The spectral sensitivity curve based on performance is markedly different from that of the retinal action potential. Owing to a limited amount of data, we would hesitate to insist that this is the exact form of the dark-adapted visibility curve, but its regularity suggests that at least the gross features possess some validity. A reason for the difference in observed spectral sensitivity may be that the behavioral study was conducted with very weak light, while very intense stimulation is required for the ERG. The stimulus brightness used in the ERG apparatus is estimated to be in the vicinity of 10,000 ft.-L. (10), while that of the discrimination box was some 9 log units less. If ERG data could be obtained with weak stimuli, or if behavioral data could be obtained with intense stimuli, spectral curves might be more nearly alike.

Although it is generally stated that the turtle possesses daylight-vision mechanisms only, we may recall that rodlike structures have been recently described (7, 14, 15). Both the smooth B wave and the performance curve suggest that these units are of some functional value.

It is not strange that activity associated with these relatively rare structures does not produce a more appreciable electric effect. In the human eye, photopic mechanisms produce only a minor electrical response which, under most conditions, is completely dominated by a much larger scotopic effect (13). An interpretation of this result is that scotopic receptors and their associated structures are quite numerous and, hence, produce large electrical responses. The limited population of photopic units cannot produce such an output. Yet it plays an important part in ordinary visual activity. The situation is reversed with the turtle retina. Although the electroretinogram reflects properties of those structures which occur in greatest numbers in the retina, these are not necessarily the only ones which may be used in behavior.

SUMMARY

The electroretinogram of the turtle was recorded using conventional techniques. Records were examined in regard to wave form, changes with stimulus intensity, and relative spectral sensitivity. With one animal, a study of spectral sensitivity based on its performance in a discrimination box was made in addition.

The findings were that the electroretinogram manifests a series of positive waves in addition to a smooth, positive, B-wave component. Waves become more numerous and of larger amplitude with stimuli of increasing intensity. ERG spectral sensitivity measured in the dark-adapted eye is found to be greatest for long wave-length stimuli no matter whether the whole response or the individual waves are considered. Spectral sensitivity on a behavioral basis is markedly different and maximizes at a shorter wave length. These results are in agreement with the hypothesis that turtles possess both photopic and scotopic retinal mechanisms.

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Received May 5, 1953.

THE EFFECT OF PRELOADS OF WATER AND SODIUM CHLORIDE ON VOLUNTARY WATER INTAKE OF THIRSTY RATS[1, 2]

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One of the basic problems in thirst research is concerned with the means by which an animal achieves regulation of its "voluntary" water intake when subjected to varying negative water loads. As Adolph (1) has shown, the precision of this regulation varies from species to species, the rat commonly showing a tendency to ingest slightly more water than is needed to replace that which has been lost during a deprivation period. If, as seems essential, water must be transported to the cells whose dehydration is the necessary condition for thirst (Wulff, 12), the velocity of this transport should be a factor influencing the duration of drinking and the amount of water ingested during a limited period. A reasonable guess would be that the more rapidly water is absorbed in the intestine, the sooner it reaches the cells, and the less is the tendency of the animal to overestimate its water deficit.

Major factors regulating velocity of fluid absorption in the intestine are the concentration of the ingested fluid and its osmotic pressure relative to that of the extracellular fluids of the body. Rabinovitch (7) for the dog and Verzár and McDougall (10) for the rat have shown that absorption velocity is related to concentration of NaCl in the ingested fluids, being more rapid with increasing concentration to a maximum between 0.50 per cent and 0.80 per cent, then rapidly decreasing through the isotonic concentration and finally reversing direction, pulling fluids into the intestine with hypertonic solutions. Some of Rabinovitch's findings illustrate the large differences in absorption rate which may be obtained. In a half-hour period 59 per cent of a distilled water load was absorbed, whereas when the load was an NaCl solution between 0.40 per cent and 0.70 per cent, 95 per cent of the fluid load was absorbed in the same time.

Thus, a means is at hand for manipulating the rate at which a fluid is absorbed and for studying the effect of absorption rates on the animal's regulation of water ingestion. Analysis of the thirst mechanisms should profit by a technique of this kind, particularly with reference to the persistent problem of factors determining the cessation of drinking activity well before fluid balance in the intercellular space is actually achieved. The present report is concerned with the effect of passively introduced stomach fluid loads on subsequent "free" water intake of rats that have been adapted to maintenance on a 23½-hr. water deprivation. The first section presents preliminary data on preloads of varying volume of tap water, on the basis of which the constant-volume loads for the absorption experiments were selected. The second section presents the results of free intake following constant-volume preloads varying in concentration of solute. The third section is concerned with free drinking by dehydrated rats of solutions containing concentrations of solutes comparable to those in the preloading experiment.

METHOD

Animals. The animals used in this experiment ranged in age from 100 to 140 days. They were male albino rats of Sprague-Dawley stock, maintained on dry Purina Laboratory Chow constantly present in their living cages.

Adaptation to drinking schedule. Water was removed from the living cages and the animals were given ½-hr. daily drinking periods in batteries of individual drinking cages in a room at some distance from the living quarters. Animals were weighed daily immediately before being placed in the drinking boxes. This preliminary adaptation period in all experiments was ten days. At the end of this period the animals were maintaining themselves at a quite constant weight and were drinking equally constant amounts of water.

Drinking boxes and water tubes. The drinking boxes, 4 in. by 11 in. by 6 in. high, were constructed of wood with a hinged wire top and with guillotine doors separating the rat from the drinking spout. The drinking tubes were 100-cc. eudiometer tubes into which are

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[1] This research was supported and made possible by funds from the Graduate Research Board of the University of Illinois.

[2] The writer wishes to acknowledge the help of his research assistant, Mr. Henry Weiss, who ran some of the animals, and of Mr. Matthew Wayner, National Science Foundation Fellow working in this laboratory, for critical discussions.

placed drawn-glass drinking tubes; the ends of these are inserted into the drinking boxes about 1 in. above the floor level.

Solutions. All fluids used in these experiments were either tap water alone or tap water used as solvent for sodium chloride. Analysis of the tap water, secured from the Illinois State Water Survey, indicated that the constituents, in parts per million, were: Fe, 0.09; Mn, 0.00; Ca, 52.80; Mg, 28.50; NH, 0.80; Na, 27.80; SiO, 18.60; F, 0.10; Cl, 6.00; NO, 0.46; SO_3, 2.30; $CaCO_3$, 300.00; total solids, 637.45. This is equivalent to a sodium ion concentration of 0.0027 per cent and a chloride ion concentration of 0.0006 per cent.

Solution concentrations used in this study are expressed in percentages, and consist of x grams of solute dissolved in 100-x cc. of tap water. Thus, a 1 per cent solution of NaCl would be made by dissolving 1 gm. of NaCl in 99 cc. of water. Solutes were weighed on an analytical balance.

Tap water was used in preference to distilled water for two reasons: (*a*) tap water was the fluid habitually consumed by the animals, and (*b*) Dennis' study (3) has demonstrated the harmful tissue effects and interference with permeability of intestinal mucosa exercised by distilled water.

Technique of stomach-loading. All fluid loads were placed in the stomach by means of no. 8 French latex catheters attached to 25-cc. calibrated pipettes. Because velocity of absorption was the variable being investigated, Verzár and McDougall's warning (10) concerning the effect of emotional stimulation on absorption was heeded and the animals were lightly etherized before the stomach tube was inserted. This was used in preference to the methods of loading described by Machella and Griffith (5), although it is possible, but not established, that the additional struggle and resistance of the latter methods might have made little difference in the results. The fluid was transferred from the pipette by gravity flow at a rate of about 0.4 cc. per second. When the desired amount had been loaded, the tube was removed and the animal carried to its drinking box. The *S* usually had complete muscular relaxation at the time it was placed in the box. Recovery took place rapidly, and by the end of the standard 15-min. delay period the animal was active and was maintaining an alert orientation toward the door separating it from the drinking tube. After the 15-min. delay the door was opened and the animal allowed its usual ½-hr. drinking period.

Experimental design. In most of the experiments to be reported the fluids were administered according to a latin-square design, each animal receiving each dosage variant in a randomly determined order. Each dosage day was followed by two days of ordinary deprivation and drinking as in the adaptation period. Preliminary experimentation showed that this two-day interval drastically reduced the "days" variance.

EXPERIMENT 1: THE EFFECT OF PRELOAD VOLUME ON WATER INTAKE

Nineteen animals were given preloads of tap water of the volumes 0, 3, 5, and 7 per cent of the immediate preloading body weight. Each animal received each load, the order of treatment being randomized prior to the experiment. A two-day interval of normal deprivation with ½-hr. drinking was interpolated between each treatment day. The upper load volume is near the top limit of normal water intake for animals of this age and weight range when on 23½-hr. deprivation. One-half-hour free drinking was allowed after a 15-min. delay at each load level.

The results are summarized in Figure 1. Free drinking is depressed as a linear function of the preload volume. However, it is interesting to note that the animals consistently overshoot the volume that would be predicted on the basis of their nonloaded intake. Their absolute "error" in estimating the volume of preload increases with the size of the load, thus looking very much like the typical errors of estimate met with in the measurement of any sensory capacity. The Weber fraction, secured by dividing the difference between total water under zero load conditions and total water under the respective load conditions by the volume of the load, approximates 0.3, being 0.28, 0.27, and 0.35 for the 3, 5, and 7 per cent loads. While more work is clearly needed to make this result interpretable, it seems possible that the rat is discriminating the volume of the load and not the decrease in negative water balance; if the latter were true, the error of estimate should be less rather than more as the size of the preload is in-

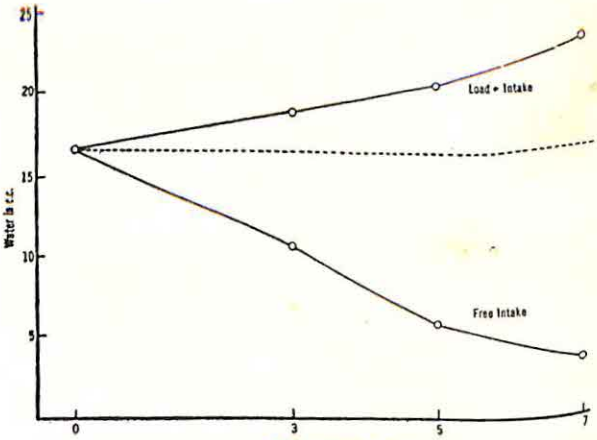

FIG. 1. Water intake of 23½-hr. deprived rats following varying volumes of water preload. The mean volumes of load corresponding to the 3, 5, and 7 per cent of body weight were 8.34, 14.38, and 20.03 cc., respectively.

creased. Since the delay period between preload and access to the drinking tubes was held constant, it is likely that the amount of water absorbed from the gut was also constant under all loading conditions, thus giving no cellular hydration advantage to the greater loads. This should lead, however, to stomach distention cues favoring a lesser error of estimate at the greater loads. Work in progress, to be reported in a later paper, may serve to clarify the question. For our immediate purpose, however, it appears that a preload of 3 per cent body weight would be a suitable volume for study of absorption phenomena. A 3 per cent load depresses the drinking of our 23½-hr. deprived animals by about 36 per cent, thus leaving an appreciable amount of water intake for the free drink period. The 3 per cent load also has the advantage of being an amount that is readily loaded into the rat's stomach without the danger of "overfilling," which is constantly present with the higher loads, particularly the 7 per cent.

EXPERIMENT 2: THE EFFECT OF CONSTANT VOLUME PRELOADS VARYING IN NaCl CONCENTRATION ON SUBSEQUENT FREE INTAKE

In a preliminary experiment the concentration of NaCl in the predrink load was varied over a range extending from 0 per cent to 3 per cent with volume of load held constant at 5 per cent of body weight. Because of deaths from various causes (pneumonia and imperfect loading technique accounting for the majority) the number of animals receiving a given NaCl concentration varied from 1 to 4, and ordinarily the entire data of such an experiment would be discarded. Certain of the results, however, suggested the later experiments in this section and should be briefly noted. The results are presented graphically in Figure 2. The interesting point to notice is the elevation of voluntary intake following the 0.5 per cent and 0.75 per cent preloads. Because of the established fact of more rapid water absorption under these particular hypotonic NaCl concentrations, our prediction had been that the voluntary intake would be depressed in this range. The relatively enormous increases in voluntary intake following the hypertonic loads of NaCl concentration from 1.0 per cent to 3.0 per cent was expected, since in this range the absorption gradient is reversed and water is being pulled into the intestine by the load. Because of the few animals at each of the points no statistical treatment of the results was possible. Accordingly, another group of 20 animals was adapted to deprivation in the manner previously described, and a 3 per cent body-weight preload was varied over the NaCl concentrations of 0.0, 0.25, 0.50, 0.75, and 1.00 per cent. The order of administration was varied systematically, the animals being assigned at random to four latin squares, and the order within the squares assigned by a table of random numbers. The total, treatment, and residual mean squares for the four replications were tested for homogeneity; because the chi squares were not significant, the replications were combined as shown in Table 1. It is evident that the NaCl concentrations of the constant-volume preloads introduce significant changes in subsequent voluntary water intake. Significance tests showed the voluntary intake following all concentrations of NaCl save the 0.25 per cent to be significantly higher than the intake following a plain water preload.

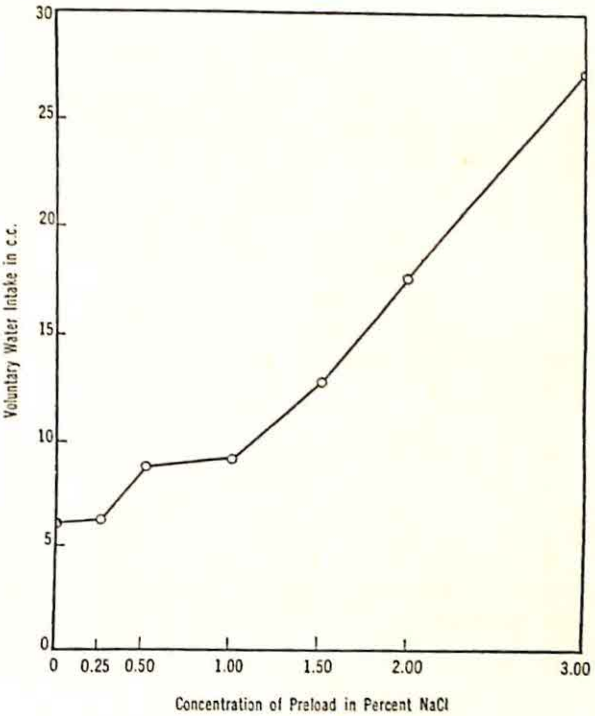

FIG. 2. Voluntary water intake of 23½-hr. deprived rats following preloads of varying concentrations of NaCl. The volume of the preload is constant at 5 per cent of body weight.

It is clear from these results that, contrary to our expectation, conditions favoring more

TABLE 1

Summary of Analysis of Variance: Free Water Intake following Constant-Volume Preloads of NaCl

SOURCE	*df*	MEAN SQUARE	*F*	*p*
Rats	19	28.43	12.46	<1%
Days	4	45.55	19.98	<1%
NaCl concentration	4	130.61	57.28	<1%
Error	72	2.28		

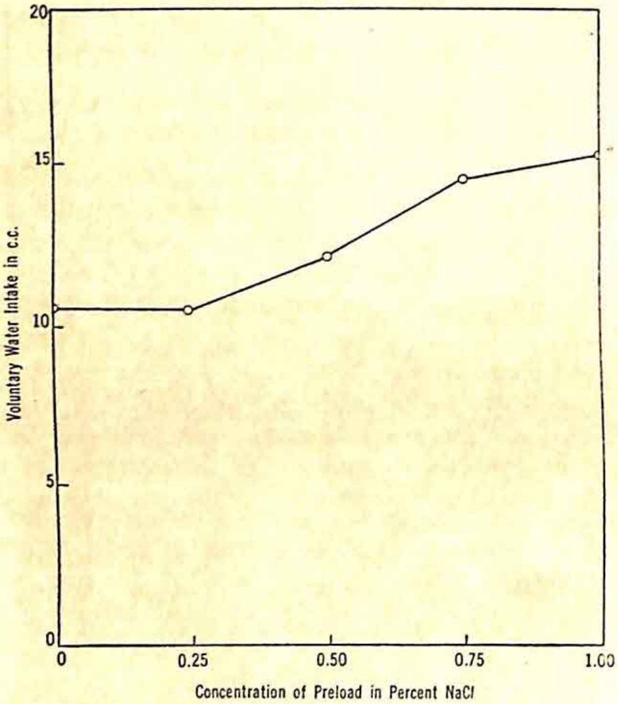

FIG. 3. Voluntary water intake of 23½-hr. deprived rats following preloads varying in concentration of NaCl. The volume of the preload is constant at 3 per cent of body weight; this represented approximately 8.20 cc. as a mean volume of preload.

rapid water absorption do not necessarily lead to more rapid inhibition of the drinking response. Indeed, precisely the opposite conclusion seems indicated by the data. While there appears to be no basis for doubting the theory that cellular dehydration is the fundamental condition for thirst, one must, in the light of results such as these, question whether transport of water to the extracellular fluid is the sole condition for inhibition of thirst. Simple osmotic calculations are of little help, since our results show an increased voluntary intake following loading with solutions that fall in both the hypotonic and isotonic concentration range. Passage into the extracellular space of NaCl solutions of isotonic concentration should not, on a simple osmotic basis, draw water from the cells, but should, assuming normal kidney clearance of the excess chloride, lead to appreciable increments of cellular hydration. Hypotonic solutions of NaCl in the extracellular space should lead to even more rapid hydration of the cells, and with less dependence on excretory balance of the excess chloride. But the experimental results show the inadequacy of such an explanation. If isotonicity of NaCl solutions were to be defined in terms of thirst inhibition rather than in terms of water equilibrium across the membranes of the erythrocyte, isotonicity for the rat would have to be moved from 0.85 per cent down to something close to no salt at all. In fact, one might make a tentative generalization that the inhibition of drinking under our experimental conditions is inversely related to the concentration of NaCl in the predrink load. Until we have further information on the velocity of salt clearance by the kidney of the 23½-hr. deprived animal, and can relate such information to our measures of thirst, the present results must remain unexplained. It is of some interest to note, however, that Rabinovitch's (7) data on the rate of intestinal absorption of NaCl solutions in the dog presage some such dilemma as this. He measured the fraction of a standard load of solution placed in an intestinal loop of dogs that had been absorbed at the end of a ½-hr. period. Although the isotonic point is roughly at 0.9 per cent NaCl, the net transfer of water *out* of the intestine was still proceeding past a concentration of approximately 1.5 per cent NaCl, and the direction was not reversed until a concentration of approximately 2 per cent NaCl had been attained.

It is possible that sodium chloride passes through the intestinal barrier so readily that local hypertonic states are created in the plasma, and that consequent waves of relatively hypertonic fluid are carried through the blood stream into the circulation of the hypothalamus, thus affording temporary increase in "thirst excitation." This notion, at first somewhat improbable because of the rapid velocity with which extracellular fluid is commonly thought to achieve equilibrium, has some support in the work of Visscher and

Roepke (11), who found that isotonic solutions of sodium chloride or even the animal's own blood serum, when placed in an intestinal loop, rapidly became hypotonic owing to an active process of moving NaCl into the blood. Studies in progress in our laboratory on the thirst-stimulating properties of subcutaneous injections of hypertonic NaCl solutions show drinking latency and duration curves which are also consistent with the idea that NaCl diffusion in extracellular fluid is sufficiently slow to allow for local concentration gradients to appear in the circulating blood. The conditions of equilibrium with respect to water exchange between membranes and compartments of the body are not simple, but are, as Höber (4) has emphasized, a combination of passive penetration and active transfer. Further research should show how these factors combine to regulate fluid ingestion.

Another point of psychological concern is suggested by our data. Richter (8, 9), Young (13, 14), and Bare (2) have reported a number of determinations of rats' preference for salt solutions of varying concentration. There is substantial agreement that rats drink most readily of solutions between a concentration of 0.5 per cent and 1.00 per cent, preferring these solutions to tap water and to more concentrated salt solutions. It is a curious fact that the preference maxima occur at the hypotonic concentrations at which there is the most rapid fluid absorption. While this may be entirely coincidental and irrelevant, the increase in tap water ingestion in the present experiment shows the same type of dependency on the concentration of the NaCl preload. It is possible that the observed ingestion preferences of rats for saline solutions are not entirely a matter of taste receptor reaction nor of some higher process of hedonic tone, but that they may also be partially reduced to factors related to speed of clearance of substances from the digestive tract. The attractiveness of this hypothesis is not lessened by noting that Magee and Reid (6) found that the absorption of glucose is most rapid from a 13.5 per cent solution for dogs, and that its absorption velocity decreases rapidly on either side of this concentration. The taste preference for glucose in the rat, as determined by Richter (8), is between 9 per cent and 10 per cent, and Verzár and McDougall (10) have determined that a 10.68 per cent solution of glucose is about 50 per cent absorbed in half an hour, but that water volume in the intestine increased by about 50 per cent. Thus, it is possible that an exact investigation of the relationship between intestinal exchange rates and preference levels may reveal physiological variables which at least partially account for preference behavior. Other factors being equal, those substances in aqueous solution which act to dehydrate the animal may be more abundantly ingested than those that promote hydration.

EXPERIMENT 3: VOLUNTARY INTAKE OF NaCl SOLUTIONS BY THIRSTY RATS

While, in the last experiment, the animals were loaded with hypotonic NaCl solutions, their subsequent "voluntary" drinking was always tap water. Under those conditions the intake of tap water was related to the NaCl concentration of the preload that had been received 15 min. earlier. In the present experiment no preloading was done, but the 23½-hr. deprived animals were allowed to drink for ½ hr. from one of the various concentrations of NaCl used in the previous experiment.

The same animals used in the previous experiment were used here. Following the last preloading day, two days of standard 23½-hr. deprivation and ½-hr. drinking obtained. On the next day the animals' drinking tubes were filled with NaCl solutions of percentage concentrations of 0, 0.25, 0.50, 0.75, and 1.00, the order of presentation of each solution being determined by the use of the same latin-square arrangement used in the earlier experiment. A single stimulus technique was used, each animal getting his total daily intake from but one concentration of saline. Each day of "salt"-drinking was followed by two days of water-drinking, the deprivation period of 23½ hr. remaining constant throughout the experiment. The four squares showing homogeneity of total, day, and treatment variance by the chi-square test were combined as shown in Table 2. The general trend of the results may be seen in Figure 4.

The results show some similarity to those of the preloading experiment. Again the fluid consumption is increased as a function of NaCl concentration. The biggest difference between the experiments is in the 0 to 0.25

TABLE 2

Summary of Analysis of Variance: Intake of Varying Concentrations of NaCl

SOURCE	*df*	MEAN SQUARE	*F*	*p*
Rats	19	70.29	5.92	1%
Days	4	161.28	13.59	1%
NaCl concentration	4	322.54	27.17	1%
Error	72	11.87		

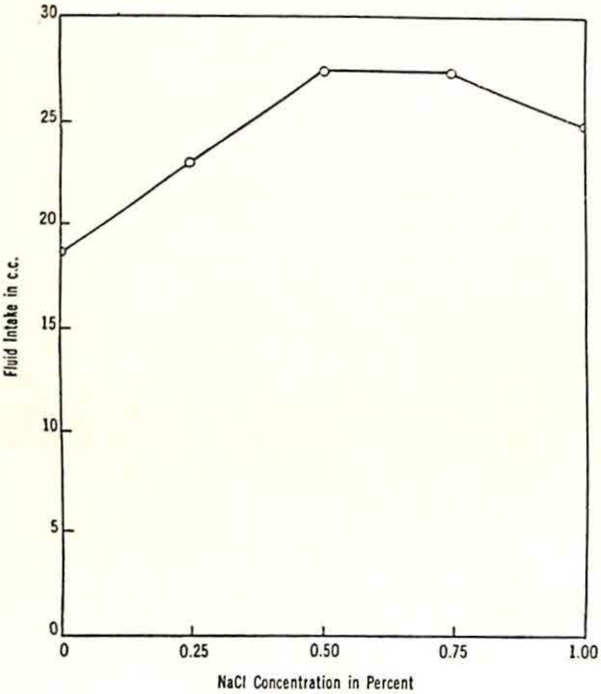

FIG. 4. Voluntary fluid intake of varying concentrations of NaCl solutions by 23½-hr. water-deprived rats

per cent solution range. In free drinking of salt solutions, the 0.25 per cent solution was consumed in greater amount than was the 0.0 per cent, although in the previous experiment the saline preload was not effective until a concentration of 0.50 per cent. Also, in the preload experiment the 0.75 per cent NaCl had significantly greater effect on consumption than did the 0.50 per cent, whereas in the free-drinking situation the differences between 0.50, 0.75, and 1.00 per cent are all of approximately chance order. It is possible that the 1.00 per cent solution is beginning to show hypertonic effect, and that tests with stronger concentrations would show that a trend toward decreased intake started from the maximum in the 0.50 to 0.75 per cent range, although Bare's (2) animals showed only a moderate decrease at 1.5 per cent.

Again, further experimentation is needed before the implication of these results can be made entirely clear. It seems likely that at least two factors are at work in determining ingestion under these circumstances. The first is an absorption factor, related to the ionic and volume exchanges in the small intestine, while the second is a "taste" factor, related to the local oral effects of solutions. It is probable that concentrations of NaCl of greater strength than 1 per cent would be ingested in even lesser amounts, in spite of the increased tissue dehydration which such solutions would produce by drawing fluid into the intestine. When these strongly hypertonic fluids are placed directly into the digestive tract they stimulate copious drinking. Such opposite effects could be obtained only if there were processes inhibitory to the ingestion stimuli occasioned by the presence of the hypertonic fluid in the intestine. It is apparent, of course, that such an inhibitory process has a high degree of adaptive utility, and that stimulation of drinking by hypertonic fluids in the intestines and inhibition of drinking by hypertonic fluids in the mouth serve the same purpose of protecting the animal against dehydration.[3]

SUMMARY AND CONCLUSIONS

The use of predrink stomach-loading techniques makes possible experimental manipulation and relative isolation of a number of the component circumstances of water ingestion in the dehydrated rat. When varying volumes of water are preloaded and the animal is allowed a ½-hr. free drinking period after a 15-min. delay, drinking is affected in the following ways:

1. Voluntary intake is decreased in approximately direct proportion to the volume of the preload.

2. If the no-preload voluntary intake is used as a reference point, the total intake (preload plus voluntary intake) increases as a direct function of the preload volume.

When fixed-volume preloads varying in

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[3] I am indebted to Professor P. T. Young for reminding me of the adaptive harmony exhibited under these varying circumstances.

NaCl concentration through the hypotonic and slightly hypertonic range are placed in the rat's stomach and it is allowed to drink tap water after a 15-min. delay, the following conclusions appear:

1. Hypotonic solutions of 0.50 to 0.75 per cent increase water intake significantly above that following preloading of the same volume of water or 0.25 per cent solutions of NaCl.

2. Hypertonic solutions of 1.00 to 3.00 per cent produce an even greater increase in subsequent voluntary water ingestion.

When thirsty rats are given NaCl solutions of varying concentration, their drinking is affected as follows:

1. Any concentration of NaCl from 0.25 to 1.00 per cent produces an increase in fluid ingestion over tap water.

2. No significantly different intakes were noted for concentrations within the range from 0.50 to 1.00 per cent, all of which were ingested in significantly greater quantities than were solutions of 0.25 per cent or tap water.

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Received March 29, 1953.

VISUAL DISCRIMINATION PERFORMANCE FOLLOWING PARTIAL ABLATIONS OF THE TEMPORAL LOBE: I. VENTRAL VS. LATERAL[1]

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Recent investigation has demonstrated that extensive bilateral ablation of the temporal lobes of monkeys produces marked impairment in their performance on visual tasks (1, 8, 13). Similar impairment, independent of visual field defects, has not resulted from lesions in other areas (1, 4, 5, 6, 9). The aim of the present study was to extend this analysis of the lesion variable by comparing the effects of partial ablations within the temporal lobe, and to begin an analysis of test and training variables by comparing postoperative measures of initial learning and of retention on a variety of visual problems.

PROCEDURE

Subjects

Eight mature baboons (animals VTH-1 and VTH-4, *Papio papio*; the others, *Papio porcarius*), whose weights ranged from 9 to 12 kg., were divided into three operate groups and subdivided into two training groups.

Surgical Procedures

The present experiment is one of a series (10, 12) in which surgical removals were made with reference to neuronographic charts. On the basis of neuronographic relationships (11) temporal cortex may be divided into three regions: *polar*, related to the anterior and limen insula and to the posterior orbital cortex of the frontal lobe; *lateral*, related to the posterior insula; and *ventral*, related to the anterior (nonstriate) cortex of the occipital lobe. The hippocampus, while not included in any of these divisions, is related afferently to at least two, its anterior extremity to the polar and the major portion to the ventral. This study compares the effects of (*a*) total temporal ablation, or "lobectomy," with those following ablations restricted to (*b*) the lateral and (*c*) the ventral division, the latter including the hippocampus. The effects of restricted polar ablations are not dealt with in this study, since lesions which have included only this portion of the temporal lobe have not produced impairment in visual discrimination performance (10).

Animals were anesthetized with sodium amytal (0.6 cc. per kg. body weight) injected intraperitoneally. The temporal bone was removed and the dura incised over the lateral surface of the temporal lobe. For lobectomies the zygoma was removed as well, in order to expose the pole, and for lobectomies and ventral-hippocampal removals anastogmotic veins were coagulated and severed to permit exposure of the ventral surface. Extirpations were made by subpial resection with a small-gauge sucker. Symmetrical bilateral operations were performed in two stages—the left hemisphere first and then the right—with two to three weeks intervening between each stage.

Lateral temporal resections were performed on LT-1 and -2. An attempt was made to extirpate the superior and middle temporal convolutions, sparing the pole but resecting as much of the banks of the superior temporal sulcus as possible. *Ventral temporal-hippocampal* resections were performed on animals VTH-1, -2, -3, and -4; the attempt was to extirpate the inferior temporal, fusiform, and posterior hippocampal gyri and the hippocampal formation. For the *lobectomies*, performed on T-1 and -2, the two partial ablations (lateral temporal and ventral temporal-hippocampal) were combined, and, in addition, the polar region, including the amygdala, was removed.

Tests

The following tests were used: visual spatial delayed response with opaque screen interposed during delay, and five visual discrimination problems, the paired discriminanda consisting of: (*a*) a plus sign and an outline square, each with an area of 3 sq. in., painted flat black on yellow backgrounds; (*b*) a cut-out circle and a cut-out square, both of wood ½ in. high and 4 sq. in. in top surface area, painted flat black and mounted on yellow backgrounds; (*c*) four horizontal stripes and a diamond, each covering an area of 3 sq. in., painted flat black on white backgrounds; (*d*) red (RT-1) and green (GT-1) Color-Aid papers (Color-Aid Company, New York, N.Y.); and (*e*) light gray (Gray 3) and dark gray (Gray 6) Color-Aid papers.

Three-inch by 4-in. plaques, serving as background for the black patterns, entirely covered by the papers, and used unpainted in delayed response, constituted the interchangeable lids of two choice-cups. The cups were spaced 12 in. apart on a sliding tray and could be concealed from the animal by an opaque screen.

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[1] Supported in part by a grant from Contract VAm23379 of the Veterans Administration to Dr. John F. Fulton. The present report covers material contained in a thesis submitted by one of us (M.M.) to McGill University, 1951, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The authors wish to express their appreciation to Drs. H. E. Rosvold and D. O. Hebb for their advice on various aspects of the study, to Miss Lila Rupp for histological preparation of the brains, and to Miss Marilyn Benson for help with the preparation of the manuscript.

A one-way–vision screen separated the animal from the *E*.

By the direct method of baiting, animals were trained on delayed response at 0-, 5- and 10-sec. delays in succession; for the retention tests, however, delays below 10 sec. were eliminated. In visual-discrimination training, the first of each pair of discriminanda was made the positive stimulus for all animals. Left and right cups were baited in a predetermined, balanced order. The noncorrection technique was employed and no punishment, other than withholding the peanut reward, was given for errors. Fifty trials a day were presented on a given test until the criterion of 90 correct in 100 consecutive trials was achieved. Postoperatively, if the criterion was not attained in 1000 trials, training on that test was discontinued.

Investigation was made also of extent of visual field, acuity, and responses to familiar objects using the methods described by Chow (4). Briefly, visual fields were determined by observing head-turning and reaching responses to a peanut moved gradually into the left or right, upper or lower, quadrants while the animal was oriented directly ahead; a second test consisted of placing several peanuts in a horizontal row and noting whether the animal consistently neglected those on either side. Visual acuity was evaluated by training the animal to pull in a peanut tied to the far end of a short length of string, and then testing for the same response using threads of successively smaller diameter. One method used for testing reactions to familiar stimuli consisted of presenting pieces of food scattered among several small wood and metal objects; unoperated animals placed in this situation select food, exclusively, after the first or second trial. Additional observations were made using trainer's gloves and net, objects which ordinarily evoke violent avoidance reactions because of methods of handling the animals prior to training.

Training Schedule

Training-Group A. The first animal in each operate group, T-1, LT-1, and VTH-1, received the delayed-response and visual-discrimination problems both preoperatively and after the two-stage bilateral removals.

Training-Group B. The five other animals were trained preoperatively only on delayed response and on the plus-square discrimination; after unilateral operations they were retested on these two problems; following the second-stage removals they were trained on all the tests. Two exceptions were made in this schedule: T-2 received interoperative training on all problems, and VTH-4 was not tested on delayed response either pre- or interoperatively. The procedure of training Group B on the last four discriminations after operation only (T-2 after unilateral and the others after bilateral lesions) permitted a comparison of their initial postoperative learning with the preoperative learning of animals in Group A.

At each stage of the experiment the problems were presented in the order in which they are described in the preceding section. Training following operation was begun two days after the unilateral and two weeks after the contralateral lesions.

The informal tests (extent of visual fields, etc.) involving no special training were presented to all animals in one daily session both before operation and after the unilateral removal. Within the first two weeks following the contralateral operation these tests were again presented in one session and then readministered at semimonthly intervals.

Anatomical Procedures

After the behavioral observations were completed, the animals were sacrificed and their brains embedded in celloidin. Coronal sections were cut at 25 mu with every twentieth section stained in aniline thionin. Reconstructions of the lesions were made from every fourth stained section. The amygdaloid complex, hippocampus, and thalamus were examined microscopically for evidence of damage or degeneration.

Serial reconstructions and cross sections indicating extent and depth of lesions are shown in Figure 1. Deviations from the intended removals may be noted. Thus, in T-1 the posterior portion of the lobe is spared on the right; in LT-2 the posterior half of the middle convolution is minimally involved bilaterally; and in the VTH group the lesions are limited in general to the middle portion of the lobe and remnants of the hippocampus (see Table 1) are spared in each. Lesions which are more extensive than intended appear in the cases of LT-2, where the anterior fusiform gyrus is damaged on the right; VTH-3 and -4, where the middle temporal convolution is invaded bilaterally; and VTH-1, where there is unilateral damage to the pole and amygdaloid complex. It should be noted, however, that these are minor deviations relative to the gross and consistent differences among the three types of lesions.

Table 1 gives the locus and extent of retrograde thalamic degeneration. The anterior half of the lateral geniculate bodies shows some involvement in all T and VTH operates, but in the majority of cases the gliosis is restricted to the ventrolateral tip of the nucleus. This finding supports the suggestion of Bucy and Klüver (2) that degeneration in the ventrolateral horn is due to interruption of a small portion of radiation fibers adjacent to the ventral cortex. More extensive gliosis, involving the posterior half of the geniculate as well, is present in the left hemisphere of T-1 and in the right hemisphere of VTH-3.

The medial geniculate bodies of the T and LT operates are only minimally involved, correlating with the incomplete destruction of the posterior supratemporal plane in these animals.

Clear signs of degeneration are present in restricted loci of the pulvinar. Thus, all animals have gliosis and loss of cells in the posteroventral portion of *n. pulvinaris lateralis*; the T and VTH operates, in the ventral half of *n. pulvinaris inferior*; and the T and LT operates, in the posteroventral portion of *n. pulvinaris medialis*. The latter finding is consistent with results obtained by Chow (3). The first two findings, however, suggest that the cortical projection fields of the posteroventral part of *n. pulvinaris lateralis* and of the ventral part of *n. pulvinaris inferior*,

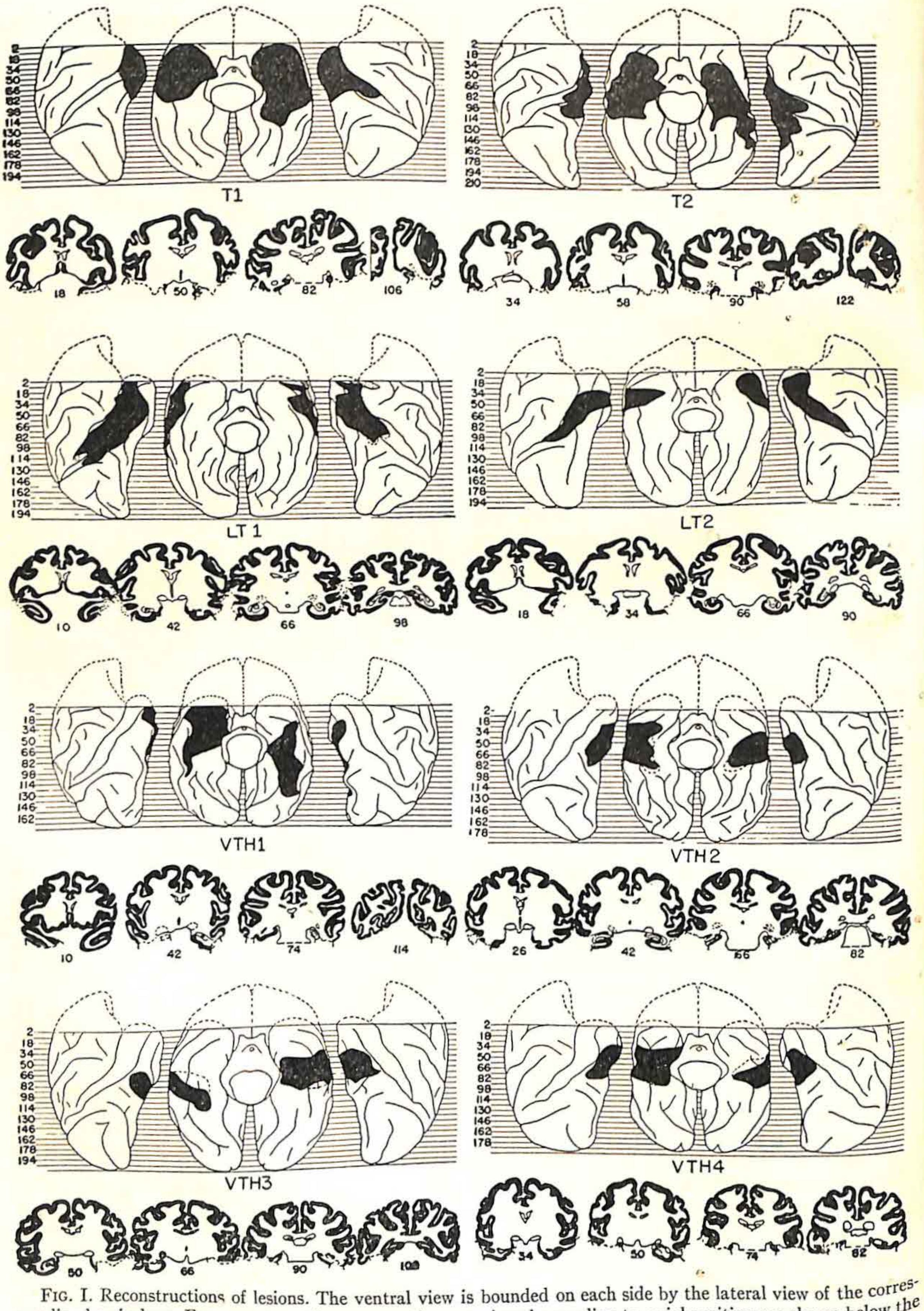

FIG. I. Reconstructions of lesions. The ventral view is bounded on each side by the lateral view of the corresponding hemisphere. Four representative cross sections numbered according to serial position are shown below the reconstructions for each animal. In the reconstructions, black indicates lesion; in the sections, black indicates intact cortex.

TABLE 1

Extent of Damage to Amygdaloid Complex and Hippocampus and Extent of Retrograde Degeneration in Geniculate Bodies and Pulvinar

AC, amygdaloid complex; H, hippocampus; LG, lateral geniculate bodies; MG, medial geniculate bodies; PL, *n. pulvinaris lateralis*; PI, *n. pulvinaris inferior*; PM, *n. pulvinaris medialis*; a, anterior; p, posterior; pv, posteroventral; v, ventral. Extent of damage and of degeneration is indicated as follows: C, almost complete; L, large; S, small; ?, small doubtful; —, none.

ANIMAL	HEMISPHERE	AC	H	LG a	MG p	PL pv	PI v	PM pv
T-1	rt.	C	C	S	—	S	S	L
	lt.	C	C	L	?	L	C	L
T-2	rt.	C	C	?	?	L	S	L
	lt.	C	C	?	S	L	C	L
LT-1	rt.	—	—	—	?	S	—	L
	lt.	—	—	—	S	?	—	L
LT-2	rt.	—	—	—	—	L	—	L
	lt.	—	—	—	S	S	—	L
VTH-1	rt.	L	C	?	—	S	S	—
	lt.	—	C	—	—	L	L	—
VTH-2	rt.	—	L	?	—	S	S	—
	lt.	—	L	S	—	S	L	—
VTH-3	rt.	—	L	L	—	L	L	—
	lt.	—	L	S	—	S	S	—
VTH-4	rt.	—	C	S	—	S	S	—
	lt.	—	L	?	—	S	S	—

which in Chow's analysis overlap in the lateral temporo-occipital area, probably extend to the ventral temporal cortex, as well.

RESULTS

Informal Tests

For several days following bilateral removals both T-1 and T-2 were unusually responsive to visual stimuli. Repeated manual and oral examination was elicited even by trainers' gloves and net, stimuli which were clearly aversive previously. This hyperreactivity, appearing also in their responses to the test plaques and thereby temporarily interfering with their performance on delayed response, abated a few days after training was begun. However, repeated indiscriminate selection of food and nonfood objects persisted for nearly three months in both animals. The only other operates that showed alterations on informal testing were VTH-3 and -4, their postoperative responses on the visual field tests indicating a left homonymous defect (found also in T-1 interoperatively) and a central defect, respectively. Animal VTH-4 showed, in addition, a transient failure on the food–nonfood discrimination. No animal with lateral or ventral-hippocampal lesions was altered in its reactions to aversive stimuli.

Delayed Response

Results on the delayed-response problem are shown in Table 2. Animal VTH-4 failed to

TABLE 2

Visual Spatial Delayed Response

Scores are trials and errors preceding 90 correct choices in 100 consecutive trials at delays of 0, 5, and 10 sec. with opaque screen interposed during the delay. For the retention tests delays below 10 sec. are eliminated. A dash indicates that the animal was not tested at that stage of the experiment. A score of 1000 trials denotes failure to acquire the habit within the limits of training.

ANIMAL	DELAY SECS.	PRE-OPERATIVE		INTER-OPERATIVE		POST-OPERATIVE	
		TRIALS	ERRORS	TRIALS	ERRORS	TRIALS	ERRORS
T-1	0	0	0				
	5	60	24	—	—		
	10	0	0			90	42
T-2	0	30	14				
	5	280	94				
	10	390	152	90	17	120	42
LT-1	0	130	24				
	5	10	5	—	—		
	10	0	0			0	0
LT-2	0	20	5				
	5	120	42				
	10	0	0	0	0	0	0
VTH-1	0	100	67				
	5	0	0	—	—		
	10	0	0			0	0
VTH-2	0	0	0				
	5	60	22				
	10	0	0	20	6	0	0
VTH-3	0	0	0				
	5	80	34				
	10	480	112	20	4	0	0
VTH-4	0					30	13
	5	—	—	—	—	1000	303
	10						

meet the criterion within the limits of *initial* postoperative training at the 5-sec. interval. All other animals, trained preoperatively and retested at the 10-sec. delay, showed either complete retention or rapid relearning after both unilateral and bilateral removals.

Visual Discriminations

Results with respect to lesions. In contrast to this generally high level of performance on delayed response, two of the three bilateral operate groups had marked and consistent impairment on the visual discrimination problems. Scores for the plus-square discrimination, on which all animals were trained prior to operation, are presented in Table 3. The five operates retested after unilateral ablation and the two LT operates retested after bilateral ablation relearned in less than 200 trials, or in half the number they scored preoperatively. The six T and VTH bilateral operates, however, failed to meet the criterion within the limit of 1000 trials, approximately three times the median number required before operation.

TABLE 3

Visual Discrimination 1: Plus–Square

Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. A dash indicates that the animal was not tested at that stage of the experiment. A score of 1000 trials denotes failure to acquire the habit within the limits of training.

ANIMAL	PRE-OPERATIVE		INTER-OPERATIVE		POST-OPERATIVE	
	TRIALS	ERRORS	TRIALS	ERRORS	TRIALS	ERRORS
T-1	940	427	—	—	1000	491
T-2	330	126	0	0	1000	502
LT-1	390	118	—	—	190	28
LT-2	300	106	110	49	150	45
VTH-1	320	134	—	—	1000	443
VTH-2	370	145	90	21	1000	308
VTH-3	280	131	0	0	1000	478
VTH-4	440	166	110	51	1000	514

Similar results were obtained on the last four discriminations, as shown in Table 4. Within Group B, animals T-2 and VTH-2, -3, and -4 failed within the limits of postoperative testing to learn any problem but the red-green discrimination, for which they required 400 to 990 trials. The extent of these deficits is indicated by a comparison with Group A's preoperative range of 0 to 100 trials for the same tests. (That Group A's preoperative scores are not biased in the direction of rapid learning is indicated by the fact that Group A's T-1, which obtained the poorest scores on the last four tests, also amassed on the plus-square discrimination more than twice the number of trials required by any other animal.) The only evidence of impairment in the performance of T-2 interoperatively and LT-2 postoperatively, on the other hand, appeared in their initial acquisition scores of 180 and 450 trials, respectively, for the circle-square, and 270 and 400 trials, respectively, for the stripes-diamond discriminations. Both animals attained the criterion immediately on the two remaining problems.

The postoperative scores obtained by the animals in Group A provide some evidence for a greater effect from lobectomy than from ventral-hippocampal removal. Animal T-1

TABLE 4

Visual Discriminations 2 to 5

Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. T-2's interoperative learning scores are placed in parentheses in the preoperative column. A dash indicates that the animal was not tested at that stage of the experiment. A score of 1000 trials denotes failure to acquire the habit within the limits of training. Pre = preoperative; Post = postoperative; T = trials; E = errors.

ANIMAL	CIRCLE-SQUARE				STRIPES-DIAMOND				RED-GREEN				LIGHT GRAY–DARK GRAY			
	Pre		Post		Pre		Post		Pre		Post		Pre		Post	
	T	E	T	E	T	E	T	E	T	E	T	E	T	E	T	E
T-1	100	42	760	365	40	17	1000	410	0	0	750	305	20	13	1000	459
T-2	(180)	(76)	1000	465	(270)	(96)	1000	466	(10)	(5)	540	142	(10)	(1)	1000	506
LT-1	40	13	20	4	20	15	0	0	0	0	0	0	20	13	0	0
LT-2	—	—	450	187	—	—	400	168	—	—	0	0	—	—	0	0
VTH-1	10	5	1000	366	0	0	400	91	0	0	10	7	0	0	0	0
VTH-2	—	—	1000	463	—	—	1000	447	—	—	400	140	—	—	1000	407
VTH-3	—	—	1000	491	—	—	1000	491	—	—	990	456	—	—	1000	417
VTH-4	—	—	1000	500	—	—	1000	424	—	—	790	322	—	—	1000	417

relearned two discriminations only (circle-square and red-green), and these with marked deficits, whereas VTH-1 relearned three problems, two of them (red-green and light gray–dark gray) immediately. Both operates, however, were markedly inferior to LT-1, which showed complete retention on all four tests.

The results for the eight animals are consistent in demonstrating severe impairment in discrimination performance following both bilateral lobectomy and bilateral ventral-hippocampal ablation, but only slight deficit following either unilateral lobectomy or bilateral lateral surface resection.

Results with respect to training groups. Comparison of the scores of Groups A and B indicates that the procedure of training animals initially after operation yielded deficits more frequently than did testing for retention. Thus, LT-2 showed impairment in the initial learning of two of the problems on which LT-1 had complete retention. Similarly, VTH-2, -3, and -4 were markedly deficient in their original acquisition on all discriminations, whereas VTH-1 relearned two tests immediately. It is unlikely that factors other than variation in training are accountable for these differences within operate groups since animals with the same lesions obtained identical scores when conditions of training were held constant (postoperative retention on the plus-square discrimination). Comparisons between initial learning and retention following bilateral lobectomy are not possible since both T-1 and T-2 received prior training on all tasks. However, T-2's interoperative scores, indicating slight deficit in original learning but none in retention, corroborate the results obtained for the lateral and ventral-hippocampal operates.

Results with respect to the test series. In addition to demonstrating selective effects of the lesions and of the training procedures, the results suggest that the occurrence and extent of deficit are functions also of a third variable, viz., test "difficulty." Difficulty is here defined in terms of the preoperative learning rates of the three animals in Training-Group A, their trial-and-error scores decreasing consistently in the order: plus-square, circle-square, stripes-diamond, light gray–dark gray, and red-green. Postoperatively, all six T and VTH operates failed to learn the most difficult discrimination (plus-square), whereas none failed the least difficult (red-green). Moreover, the three animals (T-2 interoperatively, LT-2 and VTH-1 postoperatively) that showed partial impairment on the last four tests scored deficits consistently on the more difficult problems (circle-square and stripes-diamond), and no deficits on the less difficult (light gray–dark gray and red-green).

DISCUSSION

The behavioral alterations observed in T-1 and T-2 following bilateral temporal lobectomy confirm results obtained in the monkey by Klüver and Bucy (8) and Blum, Chow, and Pribram (1). The effects include, consistently, approach to previously aversive stimuli, indiscriminate selection of food and inedible objects, and impaired performance on visual discrimination tasks. The absence in animal T-2 of demonstrable defects either in acuity or in visual fields, and, more directly, the finding of only minimal degeneration in this animal's lateral geniculate bodies support an earlier conclusion (1) that the behavioral effects of temporal lobectomy cannot be ascribed to geniculo-striate damage.

The analysis of the effects of subtotal temporal lobe lesions shows that, whereas responses to aversive stimuli were unaltered following any of the partial resections, marked and sustained discrimination impairment independent of field defects was produced by the bilateral ventral-hippocampal ablation. In contrast, little or no discrimination deficit was obtained after any form of unilateral damage or after bilateral resection of the lateral surface.

An account of the discrimination impairment in terms of the interrelationships among the lesion, test, and training variables may be summarized as follows: With respect to retention and relearning, bilateral lobectomy produced deficits on all discriminations, bilateral ventral temporal-hippocampal ablation on difficult tasks only, and bilateral lateral surface resection and unilateral lobectomy, none. With respect to initial postoperative learning, bilateral ventral-hippocampal ablation produced deficits on all discriminations, bilateral lateral surface resections and unilateral lobectomy, on difficult tasks only.

Whereas these results indicate correlations between deficit and (*a*) lesions, (*b*) training procedures, and (*c*) test difficulty, the last relationship can only be tentative, since the test order of decreasing "difficulty" corresponds closely to the sequence in which the tests were administered. Thus, the trend toward more rapid learning on successive discriminations may have been a function of cumulative transfer effects and, postoperatively, of time elapsed since operation, rather than of a decrease in difficulty per se.

The failure of the animals with lobectomy and ventral-hippocampal lesions to react differentially to paired patterns, colors, or shades of gray appeared without concomitant impairment on delayed response. Previous results on delayed-response performance following temporal lobe ablations have been inconclusive. Blum *et al.* (1) reported complete failure to relearn the problem in one lobectomized macaque, whereas Jacobsen and Elder (7) reported perfect retention in an animal with a comparable lesion. Similarly, Chow (4) found a retention deficit in one monkey with a lateral surface extirpation but not in another. In the present experiment one baboon in eight showed impairment, and this animal, tested for initial learning, had only the partial ventral-hippocampal removal. The combined results suggest that temporal lobe lesions interfere only occasionally with performance on delayed response, and that these deficits, unlike discrimination deficits, are not consistently related either to the locus or extent of lesion or to the schedule of training.

SUMMARY

1. Two baboons with temporal lobectomy, two with lateral surface ablations, and four with ventral surface-hippocampal ablations were split into two training groups matched on the basis of lesion. One group was tested for postoperative retention, the other primarily for initial postoperative learning, on a series of visual discriminations. All animals received, in addition, the delayed-response test, visual field and acuity tests, and tests of reactions to familiar objects.

2. Following the behavioral observations the animals were sacrificed, the lesions verified, and the thalami examined for retrograde degeneration. The degeneration findings suggested an extension of the known projection field of the pulvinar.

3. Analysis of the behavioral results showed that ventral-hippocampal ablation, as well as lobectomy, in contrast to lateral resection (or any form of unilateral lesion) produced marked impairment in visual discrimination performance. Deficits occurred more frequently in initial learning than in retention and appeared to be related to test difficulty, confounded with order. With the exception of the lobectomized animals' increase in approach responses to inedible and previously aversive objects, no consistent postoperative effects were obtained with any of the other tests.

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Received May 4, 1953.

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CONTROL OF HOARDING ACTIVITY IN RATS BY THE MEDIAN CEREBRAL CORTEX[1]

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The effects of fairly large cortical ablations (23 per cent to 50 per cent of the neocortex) on hoarding activity in rats have been previously investigated (8). The experimental animals exhibited marked reductions in hoarding scores as a consequence of the operations. It was found, moreover, that the hoarding deficit was related to the extent of the lesions along the median surface of the cortex by a correlation coefficient of 0.45, which was statistically significant. The results of this investigation suggest that this particular cortical surface exerts a greater influence on hoarding behavior than do other cortical areas of similar size.

Investigations of the effects of cortical lesions on behavior patterns such as maze learning (4), maternal behavior (1), and copulation of the male (2) supported the concepts of "mass action" and "equipotentiality" of the cortex, i.e., the larger the cortical lesion, the greater the deficit of the behavior investigated, and lesions of the same size are generally equally effective, regardless of their location on the cortical surface. These reports do not indicate, however, specific explorations of the median cortical surface, which is difficult to investigate since it is located along the sagittal sinus of the brain. Exposing of this blood vessel results frequently in profuse bleeding, which may be fatal to the animal. Exploration of the median cortical surface requires, therefore, the development of operative techniques which permit this surface to be exposed, without causing excessive bleeding from the sagittal sinus.

In the present investigation such an operational technique was developed, and it was then possible to determine the effects of relatively small lesions along the median cortical surfaces on hoarding behavior in rats.

METHOD

Apparatus and Animals

A closed-alley type of hoarding apparatus, which has been previously described (8), was employed. The pellets in the hoarding bin were Purina Laboratory Chow of approximately uniform size.

Laboratory-bred albino rats (200 to 300 gm.) were used in the experiment. The females (identification numbers between 1 and 35) were of the Sprague-Dawley strain, and the males (identification numbers 36 to 47) were of the Lippman strain. A total of 54 animals were given preliminary hoarding trials of at least 10 days' duration. The 26 best hoarders were then selected for the experimental trials. No differences in hoarding activity could be observed between the two strains of rats during the preliminary trials. The weight of each rat was recorded once a week.

Hoarding Trials

The preoperative experiment consisted of 16 daily hoarding trials. Each animal was given two food pellets 40 min. before each hoarding trial, which lasted 20 min. All uneaten pellets were removed from the cages at the beginning of each trial, and the hoarded pellets were removed at the end of the hoarding trial, when they were counted and returned to the food bins. The number of pellets hoarded by a rat during one trial was its hoarding score for this trial. Pre- and postoperative trials were generally conducted at approximately 24-hr. intervals, although sometimes the interval was 48 hr. When 2 consecutive trials were 2 days apart, the animals were given their regular feeding (2 pellets) on the intervening day. No marked differences could be observed in the rats' hoarding activities between 48-hr. and 24-hr. trial intervals. This is in agreement with previous findings (7) concerning the spacing of hoarding trials between 12 and 48 hr. The daily room temperature was recorded and found to vary between 68° and 72° F. during both pre- and postoperative trials.

It has been observed (7, 8, 9) that individual rats begin to hoard at different trials during an experiment and that each rat shows irregularity in its hoarding scores during the first few days. Hoarding scores during the first days of an experiment are consequently not stable, and it was decided to consider the daily hoarding between the third and twelfth day of each rat's hoarding activity as the basis for the preoperative scores. On the basis of these scores the animals were divided into two groups of approximately equal mean hoarding scores, those which were to receive lesions of the median cortical surface, the "median group," and those which were to receive lesions of the dorsolateral cortical surface, the "lateral group."

After their operations the rats were returned to their home cages for a period of recovery. Postoperative hoarding trials began 18 days after the last preoperative trial. The former consisted of 25 trials, conducted according to the same schedule as the preoperative trials. The number of pellets collected during each of 10 trials following the second day of hoarding of each rat served as the basis for the postoperative hoarding scores. As a consequence of the operations 3 animals died. The experimental results were therefore based on the hoarding scores of 8 rats in the lateral group and 15 rats in the median group.

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[1] This investigation was supported in part by a research grant from the Hixon Fund.

Operative Procedures

The animals were operated under pentobarbital (30 mg. per kg. body weight) narcosis, supplemented by ether. Five μgm. atropine was injected in order to reduce respiratory difficulties. The rat's skull was widely exposed and small trephine holes were placed as far apart as possible in the left parietal and right frontal bones. Each hole was then enlarged by opening the skull with bone scissors, approximately from the lambdoid suture to the frontal half of the frontal bone and from the temporal bone to a strip of bone above the sagittal sinus.

In order to expose the median cortical surface, this strip of bone was removed by notching its caudal end, cutting across its frontal end, and then lifting it up until it broke off along the caudal notch. In this manner the dura above the sagittal sinus was exposed without blood loss from the sagittal or transverse sinuses. When a cautery tip was then moved over the dura above the sinuses, some bleeding ensued from these blood vessels. This bleeding could, however, be readily stopped by further cauterization. The dura overlying the median cortex was then removed and the underlying cortex was scooped out with a curette. An attempt was made to remove most of the median surface of the cortex and a minimum of lateral cortical tissue.

For the lateral group of rats the dorsal openings in the skull were further enlarged by removing part of the temporal bones. The dura was then pierced along the lateral edges of the openings and strips of underlying cortex were scooped out in each hemisphere. In two of these animals (rat 9 and one that subsequently died) the bone strip above the sagittal sinus was subsequently removed and the sinus was cauterized. After removal of the cortical strips the skin flaps were sutured and the suture was covered with collodion.

Determination of Lesions

The location and size of cortical lesions were determined according to the procedure described previously (8). The stain used was gallocyanin, which was found to color the tissues more intensely than did toluidine blue. The lesions were reconstructed on Lashley brain diagrams.

RESULTS

Effects of Lateral Lesions

The location and extent of the lateral lesions are shown in Figure 1. The size of the lesions for the group of eight rats ranged between 9 per cent and 19 per cent of the total surface of the neocortex, with a mean value of 13.7 per cent. These lesions, with the exception of the lesion of rat 9, did not include the median cortical surface. The dura of rat 9 had been cauterized above the sagittal sinus during the operation. Figure 2A shows the tracing of a brain section of rat 10 at approximately level 4.5 of the brain diagram. The areas of cortical ablation can be seen in this figure.

The magnitude of hoarding for each rat is expressed by its "hoarding score," which is the mean number of pellets collected per trial during the 10-day preoperative and postoperative hoarding periods, respectively. The mean scores for this group of eight rats were

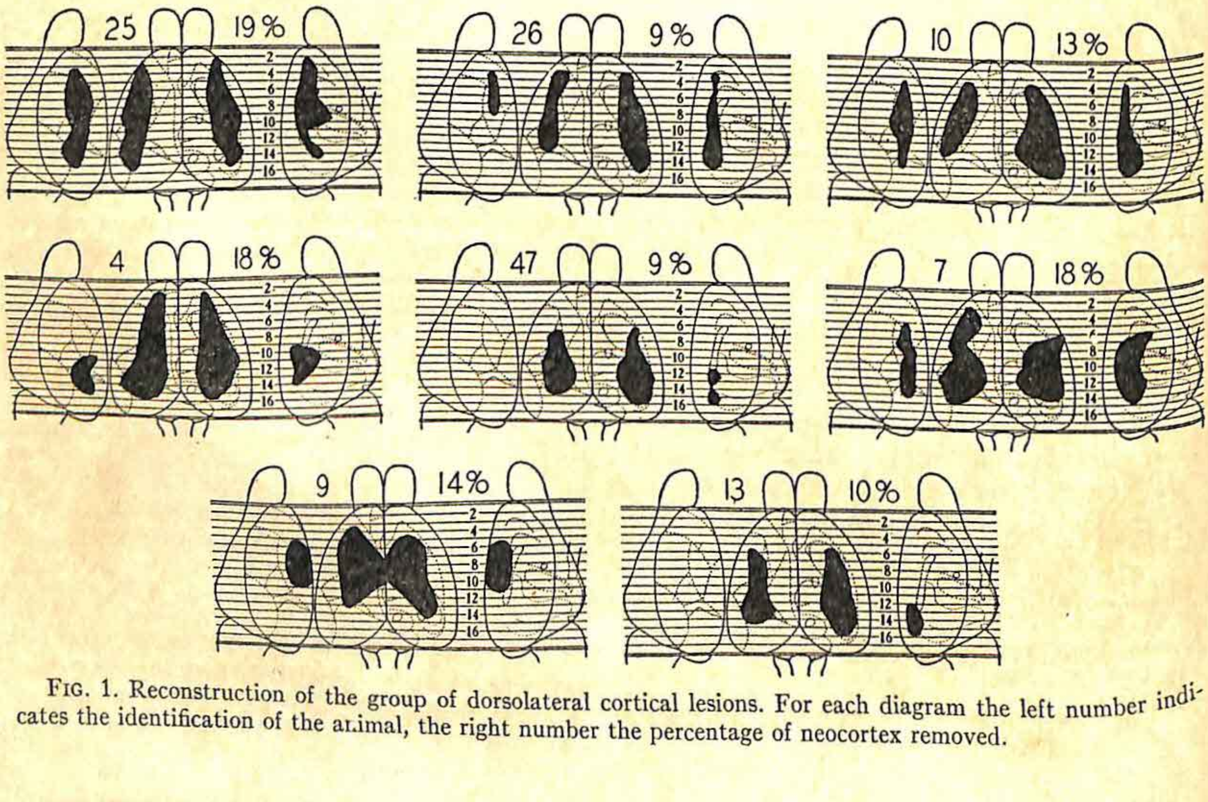

FIG. 1. Reconstruction of the group of dorsolateral cortical lesions. For each diagram the left number indicates the identification of the animal, the right number the percentage of neocortex removed.

35.8 pellets for the preoperative and 33.6 for the postoperative trials, with standard deviations of 13.1 and 7.15, respectively. These scores indicate that there was no appreciable hoarding change for this group of rats as a consequence of the operation. Two rats, however, showed substantial reductions in hoarding, which may be expressed by the "deficit index" (DI), i.e., the ratio of the difference between pre- and postoperative hoarding to the preoperative hoarding score. Rat 9, which had some tissue removed on the median cortical surfaces (Fig. 1), had a DI of 0.39. For rat 13 the DI was 0.49. The brain sections for this rat showed bilateral subcortical damage at approximately level 10 of the brain diagram. The brain sections of the other rats in this group did not indicate subcortical brain damage.

The small difference between the pre- and postoperative mean hoarding scores for the group of rats with dorsolateral lesions is not surprising, since other investigators have found that lesions smaller than 20 per cent of the cortical surface had little effect on the behavior investigated (1, 2, 4).

Effects of Median Lesions

Lesions of the median cortical surface are reconstructed in Figure 3. It was not always

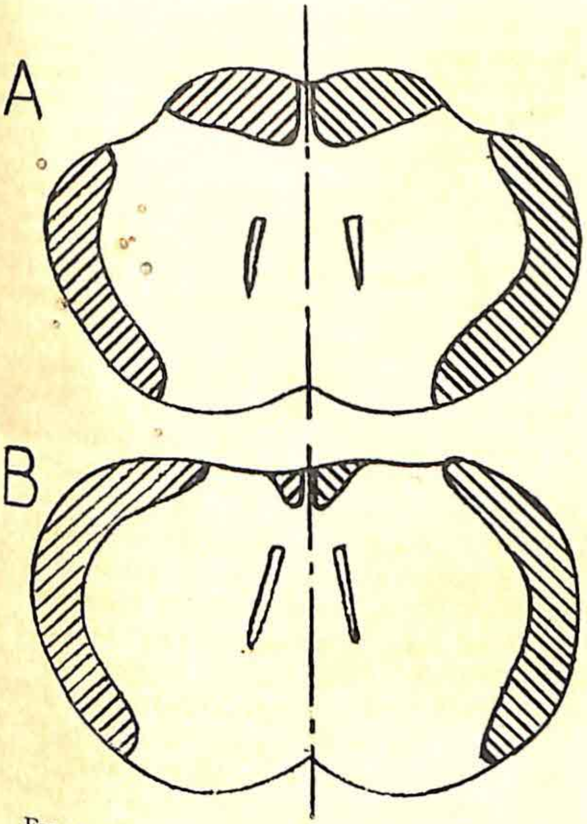

FIG. 2. Tracings of brain sections at approximately level 4.5 on the brain diagrams. A: for rat 10, in the lateral group; B: for rat 2, in the median group. The sections of cortex remaining after the operations are shown by the shaded areas.

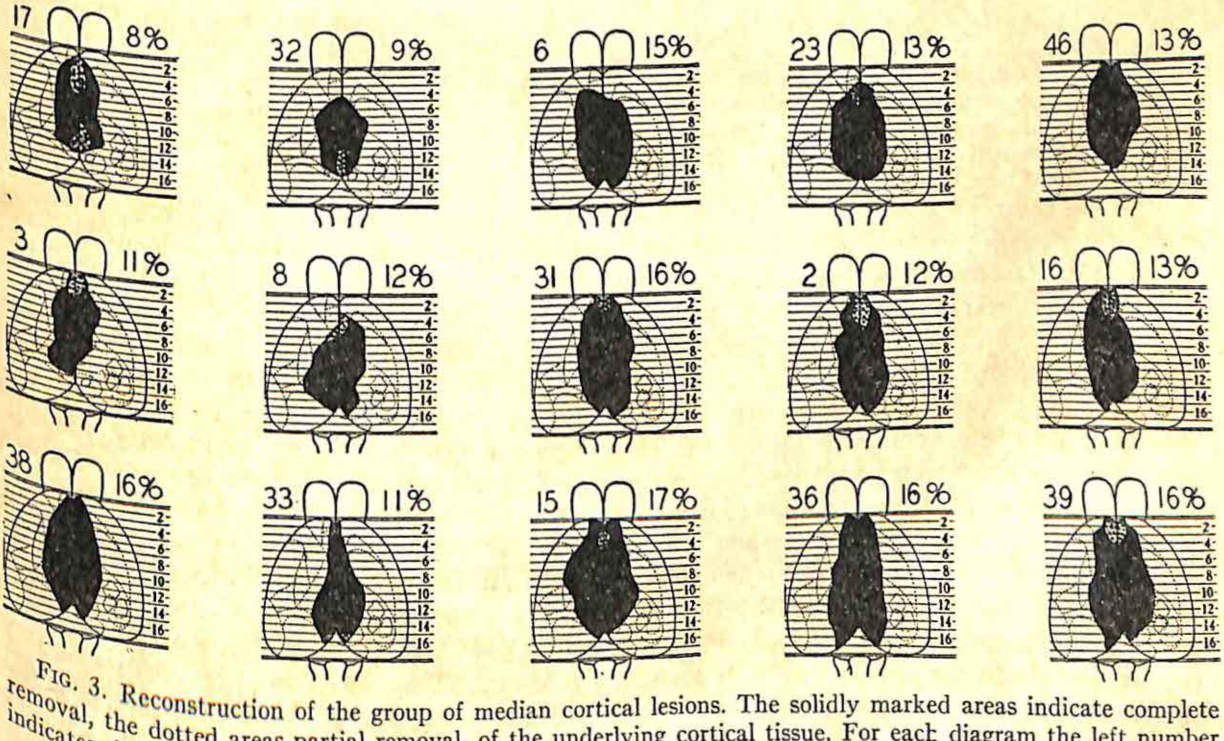

FIG. 3. Reconstruction of the group of median cortical lesions. The solidly marked areas indicate complete removal, the dotted areas partial removal, of the underlying cortical tissue. For each diagram the left number indicates the identification of the animal, the right number the average percentage of cortex removed.

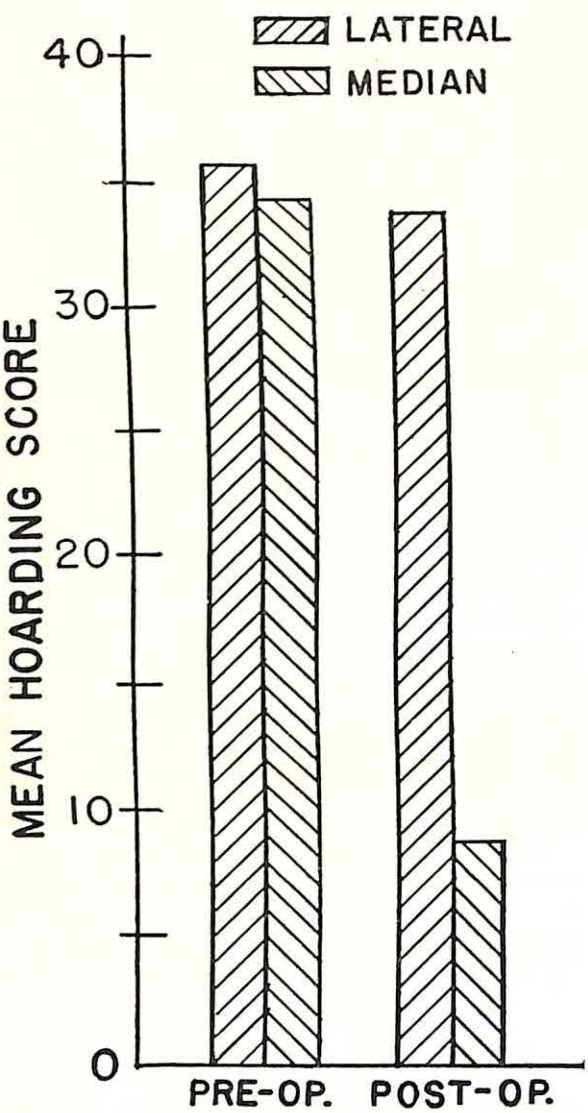

FIG. 4. Mean hoarding scores (number of pellets collected per trial) for the groups of rats with lateral and median lesions, respectively, during pre- and postoperative hoarding trials.

possible to remove all the cortical tissue along the median surfaces. The tracing of a brain section of rat 2 at approximately level 4.5 of the brain diagram is shown in Figure 2B, which indicates that small pieces of cortical tissue remained near the midline of the brain. The dotted areas in Figure 3 indicate surfaces where the underlying cortex was not completely removed, whereas the solidly marked regions correspond to surfaces where all the underlying cortex had been taken out. In order to determine the approximate size of cortical lesions, it was assumed that one-half of the cortical surfaces indicated by the dotted areas was destroyed. As can be seen from Figure 3, the dotted areas constitute only small portions of the total cortical lesions, so that this approximation may be fairly accurate. The size of the lesions for this group of rats ranged between 8 per cent and 17 per cent of the total cortical surface, with a mean value of 13.3 per cent.

An examination of the brain sections showed that rat 15 had rather extensive bilateral damage to the frontal portions of the striatum. Damage to the corpus callosum was observed in rats 3, 23, and 33. No subcortical lesions could be seen in the sections of any of the other rat brains.

The mean preoperative hoarding score for this group of rats was 34.3 pellets, with a standard deviation of 13.3. For the postoperative hoarding the mean was 8.65 and the standard deviation 5.7. Figure 4 shows the mean pre- and postoperative hoarding scores for the lateral and median groups of rats. This figure illustrates clearly the marked drop in hoarding of the median group as a consequence of the brain operation. For the postoperative hoarding the difference of 24.95 pellets between the lateral and median groups is highly significant. The *t* ratio for this difference is 8.06, which indicates a probability of less than .001 that the two groups were samples from the same population. During the preoperative hoarding trials the difference between the two groups was only 1.5 pellets ($t = 0.25$), which may well be ascribed to chance variations.

For the rats with median lesions the drop in hoarding as a consequence of the operations was significant for every rat in the group. The smallest *t* ratio for the difference between mean pre- and postoperative hoarding was 4.46 for rat 17, which is significant beyond the .01 level of confidence.

All rats in this group, except rat 39, hoarded during the postoperative trials. Rat 39 went to the food bin several times during this period, ate some pellets there, and carried several pellets in the alley, where it dropped them before returning to its cage. It may therefore be concluded that lesions of the median cortex did not interfere with the rats' abilities to perform the hoarding activity.

The DI for the group of rats ranged between 0.38 (rat 17) and 1.00, and its mean was 0.73, with a standard deviation of 0.18. If, as has

TABLE 1

Comparison of Hoarding Speeds and of Daily Latencies of Hoarding for Two Groups of Rats

VARIABLE	LESION GROUP	NO. OF RATS	NO. OF SCORES	MEAN (SEC.)	σ (SEC.)	DIFF. BETW. MEANS	
						t	p
Daily latency	Lateral	7	34	22.3	16.6	1.57	$>.05$
	Median	13	60	29.7	28.8		
Hoarding speed	Lateral	8	104	5.22	1.41	6.06	$<.01$
	Median	13	125	7.02	2.92		

been hypothesized, the reduction in hoarding is due to the removal of cortex along the median cortical surface, the amount of cortex removed along this surface may be related to the magnitude of the DI. The median cortical surface may be indicated in Lashley's diagrams by areas c, f', aa, and m' (4). The extent of the lesions along the median cortical surface was estimated by measuring their lengths along this strip of Lashley's areas in units of levels of the brain diagrams. These measures for the right and left hemispheres were then added. Again, since the total surface along the dorsal-ventral dimension was not always removed, partial lesions, which are shown by the dotted areas in the diagrams, were expressed by half-units. Since these cortical areas extend approximately between levels 1 and 17, total bilateral removal of the median cortical surface would be indicated by 32 units. The percentage of the total median cortex removed ranged between 50 (rat 17) and 97 (rat 36) with a group mean of 75. It was then possible to determine the correlation between the extent of median cortical lesions and the deficit index. These calculations resulted in a product-moment correlation coefficient of .87. The t ratio for this coefficient is 13.85, which indicates that a positive correlation exists between these two variables at a confidence level well beyond .01.

Additional Measures of Hoarding Activity

Several authors (6, 7) have discussed the complexity of the hoarding performance of rats and have pointed out that the "number of pellets collected" is only one measure for this activity. One may therefore compare the performances of the two groups of rats on other measures of this behavior.

A rat does not usually begin to hoard on the first day of an experiment, but it may remain in its cage or wander in the alley for several days prior to hoarding. The interval between the first postoperative trial and the trial at which each rat began to hoard was determined for both groups of rats. For the lateral group the mean for the trials at which hoarding began was 5.5 and the range was from the third to the twelfth trial, while for the median group (14 rats) the mean was 7.1 trials and the range was from the second to the fourteenth trial. The median for both groups was 4.5 trials.

Records were kept of the daily latency (the interval between the opening of the sliding door and the rat's first entrance into the alley in order to hoard) and the speed of hoarding (the time interval between the rat's leaving the cage and dropping a hoarded pellet in it) during the period between the twelfth and twenty-third day of the postoperative experiment (this was generally during the last five days of the ten-day trial period for each rat). Comparative values of these measures for the two groups of rats are shown in Table 1. This table indicates that not all animals were used in these observations. For the latency determinations rat 25 was excluded because it died during this period, and rat 31 was excluded because it hoarded at the most two pellets with latencies of several minutes. For the speed determinations rat 36 was excluded because it hoarded so little that reliable measures could not be obtained. Rat 39 never hoarded.

The mean daily latencies were 22.3 sec. for the lateral and 29.7 sec. for the median group. The difference between these means is not significant and is largely due to the long latencies of a few animals in the median group.

The range of latencies was from 4 to 70 sec. for the lateral and from 2 to 140 sec. for the median group. It may be noted that 22 of the 34 scores for the lateral, and 33 of the 60 scores for the median group were less than 20 sec. Consequently, the majority of rats in both groups had approximately equal daily latencies.

The mean values for hoarding speed were 5.22 sec. for the lateral, and 7.02 sec. for the median group of rats. The difference between these means is statistically significant. There were, however, several rats with median lesions which hoarded as quickly as did rats with lateral lesions. For example, 74 of the 104 scores for the lateral group were 5 sec. or less, and 43 of the 125 scores for the median group were of this magnitude. The fastest hoarding speed for rats in both groups was 3 sec., whereas the slowest speed for the lateral group was 10 sec. and for the median group 17 sec. It is apparent, therefore, that, although rats with lateral lesions hoarded on the whole more rapidly than did those with median lesions, the differences between these scores are not large and are not as marked as are the corresponding differences for the magnitude of hoarding.

The analysis of these three measures of hoarding performance indicates that rats with median lesions are able to perform the hoarding act as efficiently as do those with lateral lesions and that the main difference in the hoarding behavior between these two groups is in the magnitude of hoarding, i.e., the number of pellets collected during each trial.

DISCUSSION

The results of the present investigation show marked reductions of hoarding scores as a consequence of lesions of the median cortical surface, without substantial changes of other measures of the hoarding performance. The majority of rats in the median group retrieved a small number of pellets during each trial in an efficient, orderly manner. The median values for the number of pellets collected by rats in this group are smaller than are their means, since most rats usually collected a relatively large number of pellets for a few trials and then fewer pellets during the remaining trials, i.e., the distribution of hoarding scores is positively skewed. These rats usually retrieved a few pellets during the first minutes of each trial and then remained in their cages while eating. Those rats which hoarded heavily did not do so continuously but alternated between periods of pellet-retrieving and eating in their cages. Since all animals were on deprivation feeding, they needed to eat some of the collected pellets in order to maintain their weights, and there were no appreciable changes in the weights of rats, regardless of their group, between the start and termination of the experiment.

The effects of small median lesions appear to be markedly different from those of lateral lesions, although the average size of the two groups of lesions was almost identical. The fact that the lateral lesions had no marked effect on hoarding activity is in agreement with similar investigations of other types of behavior. Beach, for example, found that lesions of less than 20 per cent of the cortical surface had little effect on the retrieving of pups by their mothers (1), nor did lesions of this size reduce the copulating performance of male rats (2); Lashley found only small increases in errors in the maze learning of rats with cortical lesions of this magnitude (4, p. 66). In the present investigation hoarding scores were reduced by an average of 73 per cent of their preoperative values as a consequence of median lesions of an average of 13.3 per cent of the cortical surface. In order to lower measures of maternal or of male copulatory activity to this extent, it was necessary to remove more than 40 per cent of the cortical surface (1, 2).

In the previous investigation (8), when large lesions were applied over most of the cortical surface, which included only small portions of the median cortical strip, the correlation coefficient between the extent of destruction of the median cortical surface and the deficit index was 0.44. It is therefore not unlikely that relatively large lesions of the lateral cortical surface will reduce hoarding activity, although not as effectively as will much smaller lesions of the median cortical surface. In the present experiment the correlation coefficient between these variables was 0.87. This coefficient may be the expression of mass action of this particular area, i.e., more extensive destruction of the median cortical surface will result in greater reduction of hoarding activity, and there are no limited areas within this surface which specifically control hoarding behavior. In order to test this hypothesis it would of course be necessary to conduct more experiments with a larger number of animals.

The present investigation points to the importance of a restricted cortical area for the control of hoarding activity. Little is known about the functional significance of this region, except that its removal does not interfere with sensory and motor activity. It may be possible that this area performs some functions similar to those ascribed to the frontal lobes in higher mammals, and recent investigations of the limbic cortex (3, 5) in cat, monkey, and man have shown the importance of this median cortical area in regulating behavior. There may be some correspondence between the limbic cortex in higher mammals and the median cortical surface of the rat. It certainly seems desirable to investigate the function of this cortical strip in relation to other behavior patterns than hoarding.

SUMMARY

Small bilateral cortical lesions were applied to two groups of rats: 8 rats in the "lateral group" received lesions along the dorsolateral cortical surfaces, and 15 rats in the "median group" received lesions along the median cortical surfaces. In order to apply the latter lesions, an operative technique was developed which avoided excessive bleeding from the sagittal sinus. The rats' hoarding activities were determined before and after the operations. Hoarding scores were the number of pellets collected during 20-min. trial periods. The results obtained were:

1. For the lateral group of rats the mean size of the lesions was 13.7 per cent of the neocortex. This group's mean hoarding scores were 35.8 pellets for the preoperative and 33.6 pellets for the postoperative trials.

2. For the median group of rats the mean size of the lesions was 13.3 per cent of the neocortex. This group's mean hoarding scores were 34.3 pellets for the preoperative and 8.65 pellets for the postoperative trials. The difference between mean pre- and postoperative scores for each rat was, moreover, significant beyond the .01 level of confidence. A "deficit index" (ratio of reduction of hoarding to preoperative hoarding score) was computed for each rat, and this index was between 0.38 and 1.00, with a mean of 0.73.

3. The deficit index was related to the extent of the cortical lesions (i.e., lengths of lesions along the midline of the brain) by a product-moment correlation coefficient of .87, which was significant beyond the .01 level of confidence.

4. The two groups of rats were compared for additional measures of hoarding activity. The mean trial for the onset of hoarding was 5.5 for the lateral group and 7.1 for the median group. The mean daily latencies were 22.3 sec. and 29.7 sec., and the mean hoarding speeds were 5.22 sec. and 7.02 sec. for the lateral and median groups, respectively.

It was concluded that the effect of small lesions of the median cortical surfaces was to greatly reduce the amount of hoarding of rats without markedly influencing other measures of hoarding performance. This restricted cortical area therefore seems to control hoarding activity to a greater degree than do other, larger areas on the cortical surface.

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Received April 2, 1953.

BIOELECTRICAL POTENTIALS AND MENTAL EFFORT: II. FRONTAL LOBE EFFECTS

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We have previously shown (2) that mental effort, such as is involved in purely mental arithmetical operations, is accompanied by greater cardiac strain as measured by the integrated heart electrical output. In the present report we shall show that a similar technique can be used to exhibit certain cerebral increases in electrical effects.

The overwhelming number of electroencephalogram (EEG) studies has dealt only with wave pattern or the qualitative aspects of the cerebral electrical response. Many alleged significances have been attached to the various wave forms, but it seems that diagnosis purely from EEG wave form is very uncertain. In a few situations the EEG form is very helpful corroborative evidence in the presence of other facts.

For instance, Cohn (1) mentions that large and slow EEG deflections of much lower frequency than the alpha rhythm are the characteristic phenomena accompanying *any* abnormal stress on the brain, whether epilepsy, brain tumor, or other conditions. But he also shows conclusively that people who are mentally normal, and who reveal no suspicion of pathological brain condition, also show these same slow, large deflections, on *some* occasions. His atlas of EEG samples verifies this.

Kennedy *et al.* (3) claimed the discovery of a new wave form during mental calculation which they called "kappa bursts." It is doubtful if these are so unique that they can be identified with mental calculation, and in fact it is doubtful, from the appearance of the samples published, that they are in any way separable from the slow deflections described by Cohn.

However, we shall show that the predisposition for these exaggerated low-frequency wave forms to appear is a concomitant of mental effort in a good proportion of the *S*s measured, and that these large deflections produce an integrated electrical potential well above that of the resting individual.

METHOD

Nineteen *S*s were given alternate 3-min. periods of mental calculation by the method and under the conditions described in the previous article (2). The active electrode was attached over the left frontal lobe for right-handed *S*s and the right lobe for left-handed *S*s (but it is not certain that this has any significance in the final results). The neutral electrode was attached to the ear lobe which was on the same side as the active electrode. The bioelectrical output was then connected to (*a*) a Grass standard electroencephalograph and (*b*) the bioelectric integrator, as cited in the previous article.

If rest periods are denoted by the symbol R and calculation periods by the symbol W (work), a typical run would be RWRWRWRWR. The first half of this run is designated as RWRWR, and the last half begins with the middle R and is designated as RWRWR. The three rest periods are averaged together and the two work periods are averaged together to show the percentage increase due to mental effort. We can thus show whether or not there are any adaptive effects which change in the last half of a run in comparison with the first half. It was always important to begin and end with a rest period in order that an average control score would not be affected seriously by a change in the general level of output, either higher or lower.

RESULTS

Table 1 shows the percentages of increase for mental work periods as compared with rest periods for the frontal lobe bioelectrical wave integrations. The first column gives the values for the first halves of the runs, and the second column gives the values for the second halves of the runs. The *S*s are arranged in descending order from greatest total increases, in the third (total average) column, down to smallest increase. Just as in the previously reported cardiac studies, the comparison of first half with second half is presented to show any possible adaptive effects during the runs.

Figure 1 shows the corresponding EEG wave-form samples arranged in the same order as the data in Table 1. The letter *R* is at that position of the EEG where *S* was in a rest period; the letter *I* is over the 36-sec. intermission when *S* was being given the numeral for his next computational problem;

TABLE 1

Percentage of Increase for Integrated Frontal Lobe Potentials as Compared with Heart Potentials

Percentage increase of electroencephalic potentials from the frontal lobes during pure mental effort as compared with those taken during control relaxation periods. The *S*s are arranged in descending order of total output. Electrocardiac potentials are shown for comparison.

SUBJECT	FRONTAL LOBE INCREASES			CARDIAC INCREASES	
	First Half	Second Half	Total Average	First Half	Second Half
JWG	+67.1	+105.9	+86.5	+3.8	+3.1
RCB	+68.7	+76.6	+72.6	+7.7	+5.1
CS	+43.0	+40.9	+42.0		
SCL	+34.0	+35.7	+34.8	+3.5	
CGS	+23.2	+46.5	+34.8	+4.8	+6.8
LG	+25.9	+20.5	+23.2	+11.0	+2.7
VFS	+13.4	+31.2	+22.3	+6.0	+5.1
MSK	+27.0	+15.0	+21.0	+3.5	+3.3
OHA	+30.2	+11.3	+20.7	+4.8	+6.5
FOA	+21.2	+18.5	+19.8	+5.6	+4.1
RG	+8.3	+25.9	+17.1	+9.4	+0.4
RPG	+14.9	+18.7	+16.8	+7.1	+5.6
WLR	+11.7	+13.7	+12.7	+6.1	+4.6
RHS	+7.0	+14.4	+10.7	+6.6	+6.3
NS	+5.1	+5.8	+5.5	+6.2	+1.0
HEK	+4.4	+5.2	+4.8	+6.1	+5.9
WHM	+4.8	−2.8	+1.0	+6.9	+3.9
FC	+0.4	+0.6	+0.5	+0.2	−0.1
AM	−1.2	+1.2	0.0	+4.3	+6.3

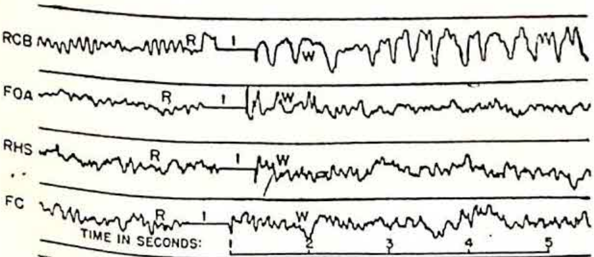

FIG. 1. Types of EEG patterns during rest and mental work. *R*, over the terminal of a rest period; *I*, over a 30-sec. intermission; and *W*, over the beginning of a mental work period. For corresponding integrations, see Table 1.

and the letter *W* is at that position where *S* was in his mental work period. Integrations were uniformly started 5 sec. after each *S* had received his problem numeral, to avoid the shock effects of auditory processes. At the end of each mental work period, integration was stopped before calling over the intercommunication speaker for the answer. The *S*s worked in very subdued light with eyes closed. The *E* watched their faces to detect signs of verbalization during the mental work.

It must be realized that these are short and very incomplete samples from graphic records which were perhaps 200 times as long. They have been selected to show, qualitatively, as good a picture of the characteristics of each *S* as can be done in the author's judgment. The wave-form characteristics of each *S* showed a strong tendency to keep the same form all the way through, even though they differed from each other quite extensively, as the chart shows.

The heavier increases in bioelectric potential are accompanied by a wave form which is typically like those of *S*s JWG, RCB, and RG, although RG generally did not have the large deflections as close together as they appear in the chart. It is possible to say that, roughly, all large bioelectric integrations were primarily due to these low-frequency, large-amplitude deflections which are similar to Kennedy's "kappa bursts."

Records like those of *S*s LG and MSK, however, show a pattern characterized by low-frequency, high-amplitude waves superimposed on the alpha rhythm, whereas in a pattern like RCB's the low-frequency form actually obliterates the alpha completely. It is probably a matter of degree.

The tracings of VFS, RPG, and WHM show a slight contamination from the tone of *m. facialis*, and this would have been greater had the electrode been a little nearer the forehead. This phenomenon is the cue cited by Kennedy *et al.*, which they asserted could be used as the "alertness indicator," but obviously it does not always appear. It is possible for many *S*s to show all the signs of mental effort without the tone of *m. facialis*.

There may be a possibility that other parts of the brain may have taken a more dominant role in *S*s, like FC and AM, whose percentage increase in bioelectric integration is very small. That is on the agenda for later investigation.

With regard to "adaptation" effects, these brain potentials show no such trends at all. Contrary to the results from the cardiac studies, the second halves actually average a slightly higher integrated potential. The average of the first halves is 21.5 per cent increase for the mental work periods, and for the second halves, 25.5 per cent increase. The difference in means is not statistically reliable owing to the very great individual differences.

There was no statistically reliable difference for problems worked correctly, problems partially correct, and problems entirely incorrect.

There was no statistically reliable correlation between the amount of the cardiac potential rise and the amount of the frontal lobe rise. This is shown in Table 1. It is safe to say merely that the bioelectrical potentials of both heart and brain are *higher* during mental effort.

SUMMARY

1. Increases in bioelectric potentials from frontal lobes during mental effort (arithmetical calculation) averaged as much as 25.5 per cent and reached a value of 105.9 per cent as the maximum.

2. The *S*s with large increases in integration exhibited wave patterns characterized by low-frequency, high-amplitude surges which sometimes obliterated the alpha rhythm during mental effort.

3. There was no reduction in potential output during the second halves of the experiment. If anything, the bioelectric output was higher.

4. There is little or no direct correspondence between cardiac potentials and frontal lobe potentials. Both are higher during mental effort.

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Received May 8, 1953.

WEIGHT JUDGMENT IN SOMESTHESIS AFTER PENETRATING INJURY TO THE BRAIN[1]

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Early investigations of sensory deficit following brain injury in man have emphasized the frequent appearance of impaired weight judgment (2, 3). In subsequent studies (1, 4), however, defects in weight discrimination were less frequently found. The apparent contradiction seems to stem, in large part, from variations in testing procedure. More recently, Teuber, Bender, and Battersby (7) studied weight discrimination in a group of 16 men with parietal lobe lesion. They found that the ability to discriminate weights was unimpaired when weights were hefted successively by the same hand, but when the weights were hefted simultaneously with both hands, significant errors appeared. These investigators, however, did not explore the separate roles of simultaneity and bilaterality, nor did they determine whether parietal lobe injury was a necessary condition for the appearance of constant errors.

The present experiment was designed to clarify the following points: whether or not (*a*) testing of both hands in the brain-injured reveals constant errors, (*b*) different effects are produced by simultaneous or successive stimulation, (*c*) constant errors appear in the presence as well as absence of somatosensory deficits, otherwise established, and (*d*) any regions of the brain are focally concerned with weight discrimination.

Groups of men with brain injury, and men with injuries to the peripheral nerves, were therefore tested to compare their abilities in weight discrimination on the supported palms.

METHOD

Subjects

Setting and criteria for selection. This study was carried out in the Psychophysiological Laboratory of the New York University—Bellevue Medical Center. The laboratory is currently engaged in research concerning the effects of penetrating injuries of the brain in man. The *S*s used in this general project consist of over 300 male veterans of World War II and a lesser number of veterans of World War I and the Korean campaign; all have traumatic lesions of the nervous system incurred in service.

Two mutually exclusive categories of *S*s have been used: men with proven loss of brain substance and men with trauma to peripheral nerves. Lesions are established by review of pertinent medical records (surgeons' notes and roentgenographic evidence). Most of the men are ambulatory, and all come voluntarily to the laboratory, where they have participated in a number of studies (5, 6, 7).

Definition of experimental and control groups. The 60 *S*s used in the present experiment were selected from those available to the laboratory. They comprised four groups of 15 *S*s each; one group with brain injury and evidence of somatosensory impairment of the hand (hereafter called the brain-injured sensory group); the second, with brain injury, but without evidence of somatosensory impairment of the hand (the brain-injured nonsensory group); the third, with injury to one or more peripheral nerves supplying the hand (the arm-injury group); the fourth, with injury to one or more peripheral nerves of the leg (hereafter called the leg-injury or control group).

Somatosensory impairment was defined by one or both of the following two criteria: (*a*) diminished *kinesthetic* sensitivity, defined as diminution of ability to discriminate the direction of small passive movements of the distal joints of the index fingers, or (*b*) diminished *tactile* sensitivity. Tactile sensitivity was determined by means of thresholds on palms and thumbs. These were obtained by the use of graded nylon monofilaments, calibrated for force exerted. The threshold was defined as the mean force just perceived in three ascending and three descending series, the method of limits being employed. A threshold was considered elevated if it was significantly greater (at the .05 level of confidence) than the mean of a normal control group.

In each of the groups used in the present experiment, one hand was considered relatively "affected," and the other, relatively "normal." In the brain-injured sensory group, the hand which showed sensory impairment (or more impairment than the other hand, if both were involved) was designated as the affected one. In the brain-injured nonsensory group, the hand contralateral to the brain lesion (or to the larger lesion, if the lesion was bilateral) was designated affected. In the arm-injury group, the hand on the same side as the nerve injury was called affected. In the control group (leg injury) the hand on the same side as the nerve injury was arbitrarily defined as affected.

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[1] Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at New York University, Graduate School of Arts and Science. The author is indebted to his sponsor, Dr. H. L. Teuber, and to Dr. Josephine Semmes for their critical guidance throughout the course of this research.

The program of research of which this investigation is a part is supported by the Commonwealth Fund of New York, and by the Office of the Surgeon General, Department of the Army under Contract DA-49-007-MD-312.

Apparatus

The stimulus objects employed in this study were two solid, circular, bronze cylinders. The total weight of each was 103.6 gm. The bases were 31.5 mm. in diameter. The top of each cylinder was attached to a universal joint, in order to allow the base of the cylinder to conform to slight inclinations of *S*'s palm. Each stimulus object was attached to a piston which moved vertically in a loosely fitted, hollow cylinder. This device caused the weight to fall on the same part of the palm on each trial. The piston was attached to an a.c. solenoid by a taut nylon cord. Energizing the solenoid caused the weight to rise instantaneously; de-energizing it caused the weight to drop instantaneously.

The solenoids were connected to a timing relay system consisting of four Hunter decade electronic timers wired in an automatically recurrent series. The timers were wired so that four different time intervals could follow one another. The last timer automatically restarted the first timer. A stimulus pair was presented in the following way: timer 2 de-energized the solenoid, causing the first standard weight to fall on the palm, where it remained for 1 sec. At the end of this time, timer 3 re-energized the solenoid, lifting the weight and keeping it up for the amount of time set on timer 3 (0.1, 2, 3, or 5 sec.). Then timer 4 de-energized the solenoid and allowed the second (comparison) weight to fall on the other palm, where it remained for 1 sec. Following this period, timer 1 re-energized the solenoid, lifting the second weight and keeping it up for the amount of time set on timer 1 (rest period).

By means of three double-throw switches the timers could be regulated so that (*a*) the weight on the right side would fall first, and the left, second; (*b*) vice versa; or (*c*) both weights would fall simultaneously.

The timers and solenoids were completely encased in double layers of felt and wood to decrease the humming and clicking usually associated with these instruments. The timers, solenoids, and stimulus objects were housed in a cabinet. The *S* sat on one side, the *E*, on the other. The stimulus objects were directly above *S*'s supinated palms, which were held securely in place inside the cabinet by restraining devices for the thumb and fingers.

Experimental Design

The experiment consisted primarily of intensity (weight) judgments between two identical objects. Throughout the entire experiment, objects of only one size and weight were employed (see *Apparatus*), and the duration of contact of the stimulus with the palm was kept constant at 1 sec. The rest period after the presentation of each stimulus pair was usually 5 sec. However, it was sometimes necessary to lengthen this period in order to allow more time for *S*'s response. At no time was *S* informed of the fact that the stimuli were physically identical.

There were three bilateral conditions of testing, two successive and the third simultaneous. In one successive condition, the affected hand received the standard, and the normal hand the comparison weight. In the other successive condition, the reverse order was used. The remaining condition consisted of simultaneous presentation of the stimuli to the affected and normal hands.

In the successive conditions five time intervals were interpolated between the standard and comparison stimuli. The time intervals intervening between the two stimuli were 0.1, 1, 2, 3, and 5 sec. All five time intervals were used in each of the two successive conditions. Thus, there were ten combinations of interval and condition, and five replications, making a total of 50 judgments in the two successive conditions.

In the two successive conditions *S* was required to judge whether the comparison (second) weight was heavier or lighter than the standard (first) weight. In the bilateral simultaneous condition he was required to judge whether the weight on the affected hand was heavier or lighter than the one on the normal hand. Only two categories of judgment were allowed in an attempt to establish in *S* an attitude of looking for small differences.

An *S*'s score for the successive conditions was the number of times in 50 judgments that the weight on the affected hand was called "heavier" than the weight on the normal hand. Each score for the simultaneous conditions was the number of times in ten judgments that the weight on the affected hand was called "heavier" than the weight on the normal hand.

In order to allow comparisons unbiased by systematic order of condition or interval, separate latin squares were set up for each *S* to randomize the three conditions and the five interpolated time intervals within each successive condition. Each of the four groups of *Ss* (brain-injured sensory, brain-injured nonsensory, arm-injury, and control) was tested under all three conditions.

RESULTS

The principal effects investigated in this experiment were those of: (*a*) *Locus of lesion*, i.e., a division of the experimental group according to the lobe of the brain injured (frontal, parietal, temporal, or occipital lobes); the right or left cerebral hemisphere; and the groups with peripheral nerve injury of the arm or peripheral nerve injury of the leg. (*b*) *Symptom*, i.e., a brain-injured group with sensory impairment, a brain-injured group without sensory impairment, and *S*s with the above-mentioned peripheral nerve lesions. (*c*) *Condition of stimulation*, i.e., simultaneous or successive presentation of stimuli.

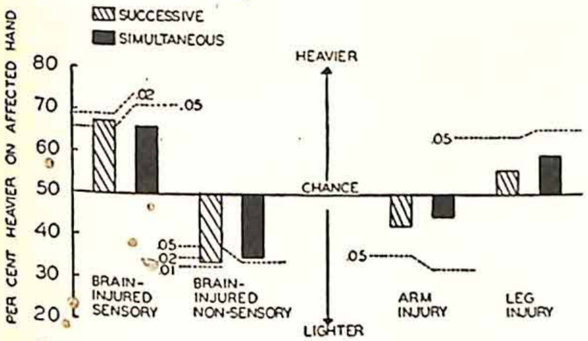

FIG. 1. Constant errors for weight judgment. Levels of significance from chance are .05, .02, .01.

Analysis by Locus of Lesion

The group of brain-injured men was divided into subgroups according to the locus of the brain lesion, comprising men with lesions of the frontal, parietal, temporal, and occipital lobes, and the right and left cerebral hemispheres. Analysis of results grouped in these ways revealed no constant errors between the hands for judgments of weights. This was true whether successive or simultaneous stimulation was employed.

Analysis by Symptom

For this analysis, the patients were classified according to their *symptoms*, rather than the presumed *locus* of brain lesion. The brain-injured population was divided into two groups: one with somatosensory impairment (as defined above) of the hand, and the other without such somatosensory impairment.

The control group, men with injury to the nerves of the leg, showed no significant constant error between the hands for weight judgment. This lack of constant differences between the hands held true for both the successive and simultaneous conditions of stimulation. Nor did the arm-injury group show any significant constant tendencies for the affected hand to perceive weights differently from the normal hand, regardless of whether successively or simultaneously stimulated (Fig. 1).

The brain-injured sensory group, in the successive condition, judged the weight on the affected hand as heavier than that on the normal hand for a significant number of trials. The brain-injured nonsensory group also revealed a significant constant error for the hand contralateral to the brain lesion. Their error, however, was in the opposite direction—they significantly *under*estimated weights on their "affected" hand with respect to the normal hand (Fig. 1).

The constant errors in the simultaneous conditions are quite similar in direction and magnitude to those of the successive conditions, but fail to be significant, possibly because of the smaller number of judgments involved.

DISCUSSION

The few investigators who have concerned themselves with the effect of brain injury upon the ability to discriminate weights analyzed their results in terms of the locus of the lesion (1, 4, 7). With the exception of Head, none of these investigators attempted to relate his findings to the somatosensory status of the patient. They have usually found that parietal lobe lesions create deficits in the ability to discriminate weights, and that lesions in other lobes are not sufficient to create these deficits. The results of the present experiment are at variance with these findings. Whereas lesion of no particular lobe was found to cause defect in weight discrimination, analysis by means of the somatosensory status of *S*s revealed two significant and opposite tendencies. Somatosensory defect of the hand created the tendency to overestimate weight on that hand. Brain injury, without concomitant somatosensory defect, created the opposite effect (underestimation) with regard to weight judgment. Had these two groups been combined into a "brain-injured" group, as has been done in most studies, the two contrary effects would have cancelled one another, and no constant error would have been manifested. This probably accounts for the negative results reported for lobes other than the parietal.

That sensory deficit per se is not a sufficient factor in the production of a constant tendency to overestimate weights is seen in the failure of the arm-injury group to manifest any constant errors. Apparently, brain injury is a necessary determinant of the constant error between the hands, and somatosensory status, of its direction.

It is difficult to relate the present findings to those of Teuber *et al.* (7). These investigators found that bilateral simultaneous hefting produced underestimation in 16 cases with parietal involvement. They did not employ bilateral successive testing, nor test men with injury to other lobes. The present study reveals that bilaterality of stimulation, but not simultaneity, was crucial in revealing a deficit. In addition, analysis of results for a parietal lobe group in the present study failed to yield a constant error, whereas analysis according to symptom revealed overestimation in the sensory group and underestimation in the nonsensory group. Direct comparison of results of the two studies may be impossible since Teuber *et al.* employed hefting, while the present study relied upon placing weights on the supported hands. In any event, both studies agree in showing that bilateral stimulation with weights can reveal constant errors between the hands after brain injury.

The physiological basis of intensity judgments in sensation is not known. However, the present findings suggest a "post hoc" hypothesis which fits the data and suggests further tests in somesthesis and other sense modalities. The hypothesis assumes that subjective intensity is dependent upon three factors: (*a*) the magnitude of afferent influx, (*b*) the number of available (functioning) neurons in the primary projection system (somatosensory cortex), and (*c*) the amount of functioning cortex outside the primary projection system.

Thus, according to (*a*), if there is a lesion in the primary afferents (peripheral nerves), the intensity should appear reduced, since a smaller than usual proportion of central neurons is activated. In accordance with this notion, our cases of peripheral nerve lesion, and sensory deficit involving the hand tested, tended to underestimate the weight.

It is postulated further that an activated proportion of the primary projection system is capable of arousing an equal proportion of the other (nonsensory) areas. If this assumption is correct, then men with lesions outside the primary sensory system (or brain-injured "nonsensory" cases) should show underestimation of the weights, since the normal number of neurons excited in the primary system activates a subnormal number of neurons in systems outside the primary area.

The converse (overestimation) occurred when sensory deficit was due to a lesion of the central projection system. A normal sensory influx impinged on groups of neurons in a system in which the total number of neurons had been diminished by brain injury. Consequently, there was a greater *proportion* of sensory neurons activated by the stimulation, hence a supernormal number of nonsensory neurons was aroused, producing overestimation of the weight. The assumption that the lesion in the projection area is focal, i.e., that more sensory than nonsensory neurons are destroyed, is essential to this point. Inspection of the brain diagrams for our sensory cases reveals that this was the case, since patients with large, widespread lesions (resulting in hemianesthesia and hemiplegia) were not testable.

The generality of this hypothesis might be tested for other aspects of somesthetic perception such as temperature or pain, as well as for other sense modalities, in order to determine whether similar results can be obtained with analogous injury groups. Specifically, the hypothesis for vision would be that if lights of equal brightness were presented to amblyopic and normal fields, in cases of lesion to the geniculo-striate system, the light in the amblyopic field should seem enhanced in brightness. In cases in which the brain injury affects cortex other than the striate area, the light in the normal field contralateral to the injury should be subjectively diminished in intensity.

SUMMARY

1. Constant errors between the hands, on estimation of relative weight with the supported hand, were determined for four groups of 15 *S*s each. These groups consisted of veterans with: (*a*) traumatic brain injury and consequent somatosensory deficit, (*b*) traumatic brain injury but without somatosensory deficit, (*c*) peripheral nerve injury of the arm, and (*d*) peripheral nerve injury of the leg (controls).

2. Two conditions of stimulation were employed: (*a*) Weights were applied to both

hands simultaneously. (*b*) The comparison stimulus was applied to one hand following application of the standard to the other hand.

3. Significant constant errors between the hands were found in both brain-injured groups. This error operated to cause relative overestimation of the magnitude of the weight on the affected hand in the group with sensory deficit, and underestimation, on the hand contralateral to the brain injury, in the group without sensory deficit.

4. A theory of the neurophysiological basis for judgments of magnitude was proposed to account for the differences among the three experimental groups. Tests of the theory in other modalities and for other aspects of somesthesis are suggested.

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Received November 6, 1953.
Early publication.

DISCRIMINATION LEARNING AND HABIT REVERSAL AS AFFECTED BY THYROID HORMONE[1]

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So far as we have been able to ascertain, two investigations dealing with the influence of hypothyroidism upon discrimination learning in rats have been reported. In one, no deviation in learning ability was found, while in the other, marked differences were noted. Rockwell (8), using a Yerkes visual discrimination apparatus with a hunger motive, was unable to demonstrate that totally thyroidectomized rats were inferior to the normal rats in learning the discrimination. Scow (9), employing a ten-choice serial discrimination apparatus with escape from water as a motive, found that even partially thyroidectomized rats were decidedly poorer learners than normal rats.

Rockwell's study dealt with habit reversal. Both thyroidectomized and normal rats were trained to approach a situation which they had previously been trained to avoid. His results indicate that the thyroidectomized group broke the old habit in favor of a new one more readily than did the controls.

We have been unable to discover any studies dealing with the influence of hyperthyroidism upon visual discrimination or habit reversal.

The purpose of this experiment is threefold: (*a*) to provide data concerning the effects of hyperthyroidism upon the learning of a visual discrimination and the reversal of that habit; (*b*) to aid in the resolution of the differences between the two existing experiments on the learning of a visual discrimination; and (*c*) to investigate the temporal course of differences in the ability to reverse a habit as a function of hyperthyroid, hypothyroid, and normal states.

METHODS AND CONDITIONS

Subjects

Sixty male Wistar rats were employed as *S*s. Their ages ranged from 25 to 35 days at the start of the experiment. The rats were divided by the split-litter technique into three groups of 20 animals each. Daily injections of 0.075 mg. of crystalline thyroxine were administered subcutaneously to the animals of the hyperthyroid group, while the hypothyroid group received 0.1 per cent thiouracil, by weight, with their powdered food ration. (Thiouracil is known to inhibit the production of thyroid hormone [1].) Treatment lasted for the duration of the experiment. The remaining 20 animals constituted the control group. In order to determine the relative effectiveness of medication upon the experimental animals in comparison with the controls, all *S*s were weighed every third day. Food and water were available in the home cages at all times.

Apparatus

A single-unit water T maze was used throughout the experiment. The alleys, which measured 8 in. wide and 14 in. long, were filled with water to a depth of 12 in. The water temperature was maintained between 22° and 24°C. At the choice point two 7½-w. electric lights were mounted 4 in. above the water surface on either side of a vertical partition which extended 2 in. into the stem of the T. A shield of plywood painted a flat black covered the choice point. Hence, when either light was turned on, only one arm of the T was illuminated, the other arm remaining in darkness. A wire-mesh ladder constituted the only means of escape from the water and could readily be attached to either wing of the T. The animal was unable to see the ladder from the choice point. From the ladder the animal could climb on to a drying platform which was fastened to the rear of the maze.

Procedure

Preliminary training. Three weeks after beginning the experimental conditions the testing program was started. On the first day all *S*s were given ten habituation trials in the maze. During these trials the electric lights at the choice point were removed. The position of the ladder was varied in a random order with five placements on each side.

Original learning. On the second day the regular learning trials were given. The lighted alley constituted the positive stimulus and thereby signified the presence of the ladder on that side. The positive stimulus was moved from one side to the other in a prearranged random order. The animals were placed in the water at the starting point in the stem of the T facing away from the discriminanda. Since the correction method was used, *S*s were allowed to swim the ladder on each trial regardless of their initial choice. Only the initial choice on each trial was counted. A choice was defined as movement of the thoracic region beyond the bifurcation of the wings. Forty trials per day were given until *S*s attained a criterion of ten consecutive correct responses. The animals were run in squads of ten; thus about 3 min. elapsed between successive trials for any given animal.

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[1] This research was supported by a grant-in-aid from the Research Council of Florida State University.

Habit reversal. When the animals reached the criterion of learning, the habit was reversed after three different intervals. Each group was divided randomly into three subgroups. One subgroup (Hypo$_1$, Control$_1$, and Hyper$_1$) from each group was trained to reverse the original habit 24 hr. after the criterion for original learning had been met. The second (Hypo$_7$, Control$_7$, and Hyper$_7$) and third (Hypo$_{14}$, Control$_{14}$, and Hyper$_{14}$) subgroups were trained on habit reversals at 7 and 14 days, respectively, after the completion of original learning. Massed training was given in sessions of 40 trials each, with an interval of 1 hr. between each session, until a criterion of 10 consecutive errorless trials was reached. Otherwise, the procedure used in habit reversal was the same as that followed during original learning.

RESULTS

Body Weight

Figure 1 shows the weight increments of the three groups. It will be seen that the growth rate of the two experimental groups was definitely retarded. The hyperthyroid group weighed significantly less than the control group 27 days after starting injections. They differed very significantly at 33 days. Likewise, the hypothyroid group weighed significantly less than the control group 20 days after instituting the thiouracil diet. This difference was very significant after 31 days on the experimental diet. Since one of the indexes of thyroid disturbance is alteration of growth rate, these data are taken as evidence that the respective abnormal metabolic conditions were established.

Original Learning

In terms of trials it was found that the Hypo group required a mean of 65.4, the Control group, 42.9, and the Hyper group, 56.4 to learn the original problem. During these trials the Hypo group committed a mean of 29.0 errors, the Control group, 19.0 errors, and the Hyper group, 24.9 errors.

A summary of the analysis of variance applied to the data of original learning is presented in Table 1. The three groups are of homogeneous variance as shown by Bartlett's test (7); the χ^2 for trials was 1.95 ($p = .40$) and for errors, 1.35 ($p = .50$). It will be noted that the F ratios for both trials and errors fall just short of significance at the 5 per cent level of confidence.

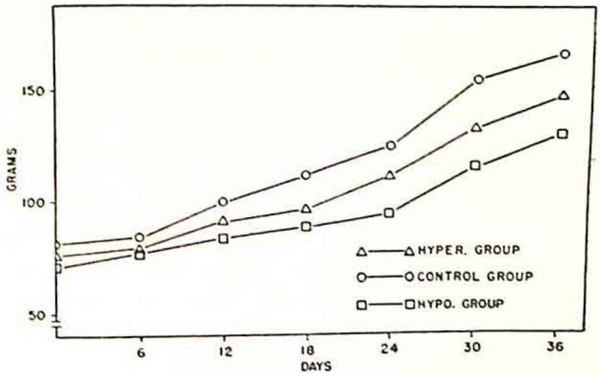

FIG. 1. Mean body weights after onset of medication

TABLE 1

Analysis of Variance of Trial and Error Scores to Learn a Brightness Discrimination

SOURCE OF VARIATION	*df*	MEAN SQUARE	*F**
Trials			
Between groups	2	2,553.0	3.11
Within groups	57	820.3	
Total	59		
Errors			
Between groups	2	506.0	2.95
Within groups	57	171.5	
Total	59		

* The F ratio required for significance at the .05 level of confidence is 3.16.

Habit Reversal

Table 2 summarizes the analysis of variance applied to the trial and error scores for reversal of the habit 1, 7, and 14 days after original learning was completed. Bartlett's test for homogeneity of variance of the nine groups for trials yielded a χ^2 of 6.43 ($p = .40$). For errors, however, the χ^2 was 15.56 ($p = .05$), causing us to reject the hypothesis of a homogeneous variance. Because of the heterogeneous variance of the error scores, only the delay differences are considered significant (7). No further analysis of the interaction was undertaken.

It will be noted that the treatment and delay F ratios for trials are significant at the 5 and 1 per cent levels of confidence, respectively. In addition, a highly significant interaction

TABLE 2

Analysis of Variance of Trial and Error Scores to Reverse the Brightness Discrimination 1, 7, and 14 Days after Original Learning

SOURCE OF VARIATION	df	MEAN SQUARE	F
Trials			
Treatment	2	3,452	4.35*
Delay	2	14,015	17.64**
Treatment × Delay	4	11,220	14.12**
Within groups	51	794	
Total	59		
Errors			
Treatment	2	924	1.66
Delay	2	3,436	6.19**
Treatment × Delay	4	1,501	2.70*
Within groups	51	555	
Total	59		

* Significant at the .05 level of confidence.

** Significant at the .01 level of confidence.

TABLE 3

Mean Trials to Reverse the Brightness Discrimination Habit 1, 7, and 14 Days after Original Learning

DAYS' DELAY	HYPO	CONTROL	HYPER	DELAY MEANS
1	54.7* *200.6*†	78.3 *44.5*	53.3 *57.9*	62.1
7	93.3 *140.5*	96.4 *112.9*	56.7 *52.8*	82.1
14	67.4 *107.3*	102.0 *166.9*	175.4 *167.8*	115.0
Means	72.6	93.0	97.2	

* Mean.

† Variance of the mean.

between treatment and delay was obtained. Further analysis of the simple effects resulting in this significant interaction was undertaken following the methods suggested by Lindquist (7). Consider, first, the influence of the treatment conditions on each period of delay, as shown in Table 3. For these purposes, let us consider the treatment conditions of hypothyroidism, hyperthyroidism, and normality as representing, roughly, the two extremes and the middle portion of a rate of metabolism continuum. The mean trials required by each group to reverse the habit after delays of 7 and 14 days appear to manifest different trends. There appears to be no effect of the metabolic level upon habit reversal at delay 1. An *F* test for the simple effects of metabolic level at delay 1 was not significant. At delay 7 the metabolic level appears to be positively related to ability to reverse the habit, whereas at delay 14 the metabolic level definitely appears to have a negative relationship with the habit reversal ability. The *F* tests of the simple effects of metabolic level at delays 7 and 14 were significant. The *t* tests showed the mean reversal trials of the Hyper$_7$ group differed significantly from the means of both the Hypo$_7$ and Control$_7$ groups. All differences between the mean reversal trials at delay 14 were significant. Highly significant interactions were obtained between treatment conditions and delay conditions at delays 1 and 14 and at delays 7 and 14. This indicates that the trend of the means of the delay 14 groups differs significantly from those of the delay 1 and delay 7 groups.

A departure from the trend of the mean reversal trials occurs in the delay 7 groups. The difference between the means of the Hypo$_7$ and Control$_7$ groups was not significant. It was not even in the expected direction to be consistent with the suggestion of a positive relationship between metabolic level and ability to reverse the habit. For this reason, the suggested trend of the means of the delay 7 groups is considered to be tentative.

Considering now the influence of delay upon each treatment condition, only one trend appears to be significant, that of the mean reversal trials of the Hyper groups. An *F* ratio of the simple effects of delay on the Hypo and Control groups failed to reach significance. Comparison of the means of the Hyper groups by *t* tests showed that the Hyper$_{14}$ group differed very significantly from both the Hyper$_1$ and Hypei$_7$ groups, but that the Hyper$_1$ group did not differ significantly from the Hyper$_7$ group. In addition, it was found that the Hyper groups showed significant interactions with both the Hypo and Control groups, while the Hypo and Control groups interacted only by chance. This supports the contention of a significantly different trend in the means of the Hyper groups from those of either the Hypo or Control groups.

DISCUSSION

Body Weight

The weight records clearly indicate that the treatment conditions influenced the growth rates of the experimental groups. The retarded growth following feeding of thiouracil to prepubescent rats is consistent with Scow's findings (9) and with other work currently being carried out in this laboratory. However, the retarded growth accompanying injections of crystalline thyroxine is contrary to the findings of other investigators (2, 4). Hammett (3) has suggested that growth change resulting from excessive amounts of thyroid hormone is a function of the size of the dose used; relatively small doses tend to enhance the anabolic process over the catabolic process, thus increasing growth rate beyond normal, whereas large doses cause the catabolic process to predominate, resulting in a decrement in the growth rate. Since the size of the injections used in the present experiment was relatively large, the retarded growth of the hyperthyroid group is interpreted as lending support to Hammett's hypothesis.

Original Learning

Analysis of variance applied to both the trial and error scores failed to show any significant difference between the Hypo, Control, and Hyper groups in learning the brightness discrimination problem. The fact that the hypothyroid animals did not differ from the normal animals is in agreement with Rockwell's results using the Yerkes discrimination apparatus, but contrary to those of Scow (9), who used a ten-choice serial discrimination problem. One possible explanation of the differences between these studies is based on the type of discrimination required of the animals. In this and in Rockwell's study a brightness discrimination was learned, whereas Scow required a pattern discrimination of his animals (horizontal versus vertical stripes). Two alternatives seem worthy of investigation in this connection: (*a*), the difference in the difficulty of the tasks, and (*b*) the effect of hypothyroidism upon the neurological mechanism. Research by Lashley and Frank (6) shows that the striate cortex is essential for pattern discrimination, whereas lower centers may mediate brightness discrimination as well as the striate cortex (5). It seems quite possible that metabolic alterations, like many drugs, may produce a profound change in cortical functioning before the lower brain centers are affected.

Habit Reversal

Rockwell found that hypothyroid rats reversed a previously learned problem more readily than normal rats. He did not specify after what period habit reversal took place. Our results confirm Rockwell's only if it is assumed that he used a delay of 14 days. This seems unlikely.

The trends of the data suggested by analysis of the simple effects in the highly significant interaction of treatment and delay were not anticipated. It would be worth while to subject these to more extensive investigation using smaller gradations of metabolism and delay.

SUMMARY AND CONCLUSIONS

Immature rats were subjected to a regime of either thyroxine injections or a thiouracil diet to determine the effects of the consequent hyperthyroid and hypothyroid states upon learning of a brightness discrimination and its reversal after 1, 7, and 14 days. The hyperthyroid, control, and hypothyroid groups, containing 20 animals each, were trained in a single-unit water T maze.

1. In original learning the analysis of variance for both trial and error scores of the three groups fell just short of significance at the 5 per cent level. There was a marked tendency for both experimental groups to be inferior to the control group.

2. With respect to habit reversal, the treatment and delay conditions had significant effects upon the trial scores. Treatment and delay interacted significantly. Analysis of the interaction suggests three trends in the mean trial scores: (*a*) a positive relationship between metabolic activity and ability to reverse the habit after 7 days' delay, (*b*) a negative relationship between metabolic activity and ability to reverse the habit after a 14-day delay, and (*c*) a negative relationship between delay and habit reversal ability in the Hyper groups.

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Received March 22, 1953.

THE EFFECT OF PROTEIN DEFICIENCY ON MAZE PERFORMANCE OF DOMESTIC NORWAY RATS

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In 1926 Anderson and Smith (1) reported the results of a study designed to determine whether inadequate nutrition would affect learning, memory, and habit formation in the white rat. Animals were taught a maze habit and then divided into three groups of 18 rats each. One group was qualitatively stunted by being placed on a low protein diet for 28 days; a second group was fed reduced rations of normal stock diet; a third group was composed of controls maintained on full rations of normal stock diet. The rate of relearning the original maze and of learning a similar maze was then measured. On completion of this practice the stunted groups were fed the control diet and grew rapidly for 20 days. A second relearning period was then instituted. Although no statistical treatment of the data was offered, Anderson and Smith stated that "... stunted rats are superior to rats grown normally in relearning a maze" (1, p. 357).

Heron and Peake (2) maintained a group of rats on a protein-deficient diet for 30 days prior to subjection to a discrimination problem. These investigators found that deprived animals learned to choose the black side of a black-white disc with great efficiency when the protein-rich goal was on that side.

Ruch (4), using adequate precautions to eliminate differential hunger drives between stunted and normal rats, found that animals whose body weights were held constant from the age of 30 days by a quantitatively inadequate diet, learned an escape-from-water maze more efficiently than rats whose diets were unrestricted or only slightly restricted.

The present study was undertaken to determine whether the use of balanced and protein-free diets as goals would affect the maze performance of animals reared from weaning to adulthood on these diets.

PROCEDURE

Forty inbred albino and hooded rats, 19 males and 21 females, weaned at 21 days of age, served as *S*s in this study. At the time of weaning the animals were divided into two groups of 20 rats each. Group C was maintained from weaning time until adulthood on standard McCollum stock diet, which consists per 1000 gm. of diet of the following: graham flour, 725 gm.; skim milk powder, 100 gm.; casein, 100 gm.; calcium lactate, 15 gm.; sodium chloride, 10 gm.; and butter fat, 50 gm. Littermates, group E, were fed a protein-free diet of the following composition: cornstarch, 70 per cent; cellulose, 15 per cent; vegetable oil, 10 per cent; salt mixture U.S.P. No. 14, 4 per cent; cod-liver oil, 1 per cent.[2] Brewer's yeast supplemented the diet of group E.

A standard commercially constructed Warner-Warden metal multiple-Y maze was used to test the effects of the foregoing diets on maze performance. This device was approximately 10 ft. long from start to goal box and contained ten cul-de-sacs. The pattern of turns employed with the maze was RLLRRLLRLR. Frequent changing of the heavy brown laundry paper on which the maze was placed reduced olfactory cues.

After one week of maze familiarization a second division of the *S*s was accomplished on the basis of the goal object or incentive to be employed on the maze problem. Ten rats in group C were run to standard McCollum diet, while the remaining ten animals in the group were provided with protein-free diet as goal object. A similar division was carried out with group E. The letters *B* (balanced diet) and *D* (deficient diet) were used to indicate the goal object to which the *S*s were running on the maze. Thus, the groups were designated ED, EB, CD, and CB.

All rats were placed on the maze following approximately 22 hr. of food deprivation. The animals were given 3 trials daily for a period of ten days, a total of 30 trials for each *S*. The rats were permitted to eat in the goal box for 15 sec. following completion of each trial. Following completion of a series of trials in any given session the *S*s were returned to their home cages and allowed access to their accustomed diets for 2 hr.

The number of errors was recorded as a measure of maze performance. An error was counted each time an animal entered a cul-de-sac, or returned toward the goal box for a distance of one body length.

RESULTS

Subnormal growth of the experimental animals as a result of the protein-free diet

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[1] A portion of this study is on file in the library of the University of Mississippi as partial fulfillment of the junior author's requirements for the degree of Master of Arts.

[2] This diet was obtained from the Nutritional Biochemical Corp., Cleveland, Ohio.

TABLE 1

Summary of the Analysis of Variance for the Four Groups of Rats

SOURCE OF VARIATION	df	MEAN SQUARE	F
Goals	1	1.3	
Diets	1	17.1	15.5*
(Cells)			
Goals × Diets	1	4.6	4.18**
Residual	36	1.1	
Total	39		

* Significant at .01 level.
** Significant at .05 level.

TABLE 2

Observed Mean Difference and t Scores Obtained between Groups with Errors Used as Criteria of Maze Performance

GROUPS	M_1-M_2	t*
EB-CB	−2.01	4.19
EB-ED	−1.03	2.53
EB-CD	−1.68	4.23
ED-CD	−0.65	1.46
CB-CD	−0.33	1.35
CB-ED	+0.98	1.71

* Values of t necessary for significance: .01 level, 2.878; .05 level, 2.101; $df = 18$.

was evident. At the time of weaning the average body weight of the controls was only 0.6 gm. greater than that of the experimentals. After 70 days on their respective diets the weights of the animals in the control group averaged 144.0 gm. in contrast to a mean weight of 56.6 gm. for the experimental group.

Table 1 gives the over-all summary of the analysis of variance for the four groups of *S*s used in the study. The goals × diets interaction variance proved significant at the .05 level of confidence with 1 and 36 *df*, respectively. The portion of the between-groups variance due to diets proved significant well beyond the .01 level of confidence. These results justified use of the *t* test for the analysis of simple effects.

Table 2 shows the results of the foregoing analysis when errors were used as the criteria for maze performance. Group EB (experimental rats run to a balanced diet) made significantly fewer errors than groups CB, ED, or CD.

DISCUSSION

The results of this experiment have indicated that the organic state of the *S*s relative to the qualitative characteristics of the goal object is reflected in maze performance. The fact that rats maintained on a protein-free diet performed better on a maze when the goal consisted of a balanced diet in comparison with littermates maintained on the same diet but running the maze to a protein-deficient goal would substantiate this statement. This finding is of particular interest in the light of the conclusions presented by Anderson and Smith (1) and Ruch (4). It will be recalled that the former investigators stressed the stunting which resulted from qualitative and quantitative dietary deficiencies in their *S*s as the etiological factor in the superior maze performance of the experimentals over the controls. Ruch (4), on the other hand, hypothesized a higher activity level in the stunted animals to account for his results. The present study group ED (experimentals run to a protein-deficient diet) was stunted equally as much as group EB (experimentals run to a balanced diet), yet the latter group was superior to the former in maze performance. It is assumed that Anderson and Smith (1) used a balanced diet as a goal object with their *S*s; hence, it would seem that these investigators might have stressed the qualitative nature of the goal object rather than the stunting factor, at least relative to the superior maze performance of their qualitatively deficient rats. The motivation factor per se might have been involved in the results obtained with their quantitatively deficient rats.

The results of the present study appear to be amenable to interpretation within the framework of the concept of homeostasis. Of all the groups used, only EB *S*s, in a condition of imbalances due to deprivation prior to maze running, or to protein deficiency, could approach adjustment through consumption of the balanced diet used as the goal object. It is, of course, recognized that the quantitative deficiency resulting from food deprivation prior to maze running may have had differential effects on the stunted and normal animals, and thus might have been a factor complicating the interpretation of the results. However, prior to further work designed to control this factor, we are inclined to emphasize the qualitative nature of the goal object relative to the organic state of the *S*s as the factor responsible for the superior performance of group EB. Group ED, for instance, might be considered as operating under the "double drive" of food deprivation and protein deficiency. Since its performance was inferior to EB's, it would seem that the possible existence of "two drives" is not sufficient, alone, to explain the superiority of group EB unless the qualitative nature of the goal object is considered.

This investigation has suggested a technique which may prove of value for future work on the maze performance of rats. Animals acquiring a maze habit would be maintained on complete dietary self-selection utilizing Richter's (3) technique for presenting the dietary choices. Their selections, quantitatively and qualitatively, would be studied prior to, during, and following mastery of the maze habit. Comparative work might be done on patterns of diet selection during extinction of the maze habit.

SUMMARY AND CONCLUSIONS

Forty domestic Norway rats were divided into two groups of 20 animals each; one group was fed a protein-free diet supplemented with Brewer's yeast from weaning until 60 days of age. The other group was fed standard McCollum stock diet for the same period of time.

One-half the animals in each group were run 30 trials on a standard Warner-Warden maze with McCollum diet as the goal object. The remaining animals ran the same number of trials on the Warner-Warden maze with protein-free diet as the goal object. It was found that protein-deficient animals running the maze to a balanced diet made significantly fewer errors than any other group.

The hypothesis was offered that the qualitative aspect of the goal object relative to the organic condition of the *S*s was the factor responsible for the above finding.

A methodological technique involving the the use of self-selection of diet in relation to maze learning with rats was suggested for future experimentation.

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Received April 9, 1953.

EFFECT OF DIFFERENTIAL QUANTITY OF REWARD ON ACQUISITION AND PERFORMANCE OF A MAZE HABIT

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The study reported here was designed to investigate the problem of effect of variation in quantity of reward upon the acquisition of the maze habit by the laboratory rat. Specifically, the experiment attempts to test the assumption that, with quality of reward remaining constant, the magnitude of an increment of habit strength per reinforcement is a function of the quantity of the reinforcing agent employed per reinforcement.

Previous experimentation, e.g., Gantt's classical study of the conditioned salivary response in the dog (1) and Grindley's study of the running time of chicks on a straightaway (2), appears to support the hypothesis that with increasing magnitude of reward there is increasing efficiency of performance in the learning situation. This work has been submitted to a critical analysis by Reynolds (4, 5, 6), who, on the basis of his own research, concludes that the positive relationship between rate of acquisition of a response and amount of reinforcement is limited to those responses which are replications of the final consummatory response. Beyond this it must be noted that these studies do not demonstrate whether the effect of increasing quantity of reward is upon the learning, or *acquisition* proper, of the habit or whether the effect is merely upon *performance* of that habit. In other words, we may raise the following query: Does the magnitude of the increment of habit strength vary directly with the increasing quantity of reward, or does increasing quantity of reward influence the amount of action potential (to use Hull's term) evoked during the learning trials? It is possible that the animal receiving a larger reward has learned no more than the animal receiving a lesser reward, but is, rather, utilizing more efficiently what has been learned during the training trials.

Examination solely of scores made during the learning trials does not allow one to determine whether obtained differences in quality of performance evidenced by two differentially rewarded groups of animals are a function of (*a*) greater acquisition of the habit by one group or (*b*) more efficient utilization of that habit. This, of course, follows from the fact that in a given situation we are able to infer the process of acquisition only from performance scores in that situation.

A solution to this difficulty can be achieved through the use of an experimental design involving transfer of training or, specifically, relearning of the original problem in the same external experimental situation but with a new drive state and corresponding new relevant reward. If we take the case when differences in the performance scores of two groups of animals receiving different quantities of reward during the learning trials are obtained, and if, after a suitable retention interval, the animals are placed again in the original learning situation but now under a different drive and with all animals receiving equal quantities of the relevant reward, then any differences persisting in the performance of the animals in the second situation may be attributed to differences in the efficacy of acquisition of the habit in the original situation. On the other hand, if the differences in the original performance do not persist, it appears feasible to attribute those original differences to variation in the utilization of the habit during the initial learning rather than to differences in acquisition per se. Relearning under a different drive state is necessitated in that, if the original drive state were maintained with the relevant reward equated, the experimental results could be confounded with the effect of raising the amount of reward for the originally lesser groups and lowering it for the originally greater rewarded groups.

METHOD

Subjects and Apparatus

The *S*s were 40 naive albino and hooded rats from the colony at Ohio State University. The apparatus used in the main body of the experiment consisted of a Stone 14-unit multiple-T maze. At four equidistant choice points there was a door which was dropped behind the rat in order to decrease the amount of time spent in retracing. These were operated remotely by *E* through the use of strings attached to the doors.

Procedure

Pretraining. The first problem encountered in the design of an experiment to meet the above specifications is that of determining whether or not the *S*s are in fact capable of distinguishing between the different quantities of reward used in the study. Accordingly, the initial step of this experiment involved pretraining *S*s on a simple single-choice T maze in order to ascertain whether or not the animals would choose the larger of the two rewards used if both quantities were equally available. The *S*s were put on a 22-hr. hunger drive with water available at all times outside the experimental situation. Following the daily experimental session, *S*s were placed in a feeding cage for 1 hr. The reward used consisted of small rabbit pellets, the smaller quantity of reward being defined as one pellet and the larger as five pellets. The larger reward was placed in the goal box at the end of one arm of the T, the smaller reward in the goal box at the end of the opposite arm of the T. The *S* was placed at the starting point, allowed to make a choice, and subsequently allowed to eat the reward corresponding to the side chosen. After four *consecutive* choices to the same goal box (either to the five- or to the one-pellet side), *S* was forced to the opposite side four times by means of a block set at the choice point. After four forced trials, *S* was again allowed to make free choices until four consecutive choices were made to one side. This procedure ensured that each *S* would have approximately equal experience with both quantities of reward, and it prevented confounding of the results with position habits. Four daily trials were given with approximately 10 min. elapsing between any two trials for a given *S*. The criterion of success in this situation was defined as 19 out of 20 consecutive free choices to the five-pellet side. It will be recognized that after every four consecutive correct choices *S* was forced to the one-pellet side four times, so that an *S* reaching criterion had been forced to the one-pellet side a minimum of 16 times. Of the 40 rats, 36 reached the criterion by the sixty-fifth trial, at which time training was discontinued for all rats. The *E* was satisfied that *S*s were capable of choosing the five-pellet reward in preference to the one-pellet reward.

Learning. In the second portion of the experiment the 40 rats were divided into two groups of 20 each by means of a combination of the split-litter technique and performance in the pretraining period. Still on a 22-hr. hunger drive, *S*s were trained in the Stone 14-unit multiple-T maze, one group receiving a one-pellet reward upon completion of a run through the maze, the other group receiving a five-pellet reward. The *S*s were given one trial daily. Each *S* was allowed approximately 2 min. in the goal box (which was sufficient for *S* to consume five pellets of food) and was then replaced in the home cage. One-half hour after the daily trial, the rats were placed in a feeding cage and allowed to eat for 1 hr. Measures were taken of time and errors on each trial.

TABLE 1

Values of t between Mean Time and Mean Error Scores of the Two Differentially Rewarded Groups

TRIALS	t FOR MEAN ERRORS	t FOR MEAN TIME
Original learning		
4 + 5	0.396	0.072
9 + 10	0.134	1.957
14 + 15	0.712	1.697
19 + 20	0.269	2.186*
Relearning		
1	0.741	0.758
2	0.256	1.270
3	0.625	0.029
4	0.438	0.252
5	0.000	0.431

* Significant at the .05 level of confidence.

Transfer. After 20 trials, training was discontinued for a period of two and one-half months. At the end of this interval, all *S*s were placed on a 22-hr. thirst drive. Each *S* was given three trials, one per day, on a straightaway leading to a goal box containing a water bottle. The *S* was allowed to remain in the goal box until it discovered and drank from the water bottle. After this familiarization with drinking in the goal box, *S*s were returned to the multiple-T maze and given one trial per day for five days, this time receiving a water reward. Each *S* was allowed to remain in the goal box until it had stopped drinking, when it was removed and placed in the home cage. Half an hour after the daily trial *S*s were given access to a water bottle for a 1-hr. period. Time and error scores were taken on each trial.

RESULTS

The time and error scores of each *S* on trials 4 plus 5, 9 plus 10, 14 plus 15, and 19 plus 20 were determined and the t test of significance applied to determine if the differences between the two groups at each of these four points on their respective learning curves were larger than those which might have been expected on a chance basis. The t test was also applied to the mean error and time scores made by the two groups on each of the five relearning trials.

During the initial learning trials, no significant differences in mean errors made by the two groups were found, the largest of the four t's not exceeding the .4 level of confidence. However, later in the learning trials, especially on the combined trials 19 and 20, a difference was found in the mean time scores which was significant at the 5 per cent level. Although this could be a chance difference, it might also be predicted from Hull's theory (3). He assumes that the differential influence of amount of reward, operating through r_g, would require a number of trials before its effect would be manifested throughout the entire maze.

No significant differences were found in either mean error or mean time scores of the two groups on any of the five relearning trials.

CONCLUSIONS

The results of this experiment indicate that although by the twentieth trial there was a significant difference in running time favoring the group receiving the larger reward, there were no significant differences in mean number of errors. Insofar as error scores were not found to be a decreasing function of amount of reward, these data do not support the hypothesis that quantity of reward influences growth of habit strength per se. Further, the findings that any differences in time scores made by the two groups disappeared when *S*s were returned to the original learning situation under a different drive state with quantity of reward equalized, tends to support the contention that quantity of reward does not affect acquisition of the habit but, rather, affects utilization or action potential of that habit.

SUMMARY

1. Forty albino and hooded rats were trained to differentiate between a one- and a five-pellet reward placed on the ends of opposite arms of a single-choice T maze.

2. After the *S* had reached criterion or had had 65 trials, it was placed in one of two differentially rewarded groups and given 20 trials, one per day, in a Stone 14-unit multiple-T maze. Both groups were on a 22-hr. hunger drive.

3. Two and one-half months following the twentieth trial, *S*s were placed on a 22-hr. thirst drive, familiarized with drinking in a goal box, and then were given five relearning trials in the multiple-T maze. All *S*s remained in the goal box until they had finished drinking.

4. No significant differences between mean error scores were found in the original learning situation. By trial 20, there were significant differences between the two groups in terms of mean running time, favoring the group receiving the greater reward.

5. No significant differences were found in either mean errors or mean time scores of the two groups during the five relearning trials.

6. These data do not support the hypothesis that quantity of reward affects the acquisition of a habit per se, but may be interpreted as suggesting that the quantity of reward influences action potential or utilization of the habit.

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Received March 18, 1953.

EFFORT AND RESISTANCE TO EXTINCTION OF THE BAR-PRESSING RESPONSE

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The concept of I_R was postulated by Hull (2) to relate lesser amounts of work or energy expenditure to the inhibition of such molar response tendencies as locomotion, "right turn," and bar pressing. As such, it offers a convenient theoretical tool in accounting for spontaneous recovery, experimental extinction, and other allied inhibitory phenomena in infrahuman experimental situations where effector impairment or fatigue would not otherwise be considered a relevant variable.

Empirical evidence for the existence of a relationship between lesser amounts of work and the magnitude of the inhibition generated is extremely tentative despite its common acceptance and frequent use. Solomon (6), in a review of the literature, has criticized most of the early studies for failure to control adequately such variables as delay of reinforcement, habit strength, and complexity of the tasks involved. The Mowrer and Jones study (4), which Hull offers as "convincing evidence" (2, p. 279) and upon which he based the quantification of the relationship of energy expenditure to the accumulation of I_R (2, p. 280), has also been seriously criticized (1, 5). The Mowrer and Jones training schedule, in contrast to what Hull reports, resulted in a far greater number of reinforcements and a higher rate of responding by rats to a bar requiring less effort to push. As a consequence, the results of the study offer an alternative interpretation, namely, that the obtained differences were due to differences in habit strength of the different bar-pressing habits.

Applezweig (1), in attempting to control for habit strength prior to extinction, utilized a design that resulted in an extreme selection of *S*s in some groups. His design also required the assumption that rats trained to push a lighter bar can be made to push a heavier bar with facility equal to that of rats trained on heavier bars and then required to push lighter bars. However, if trained to push a heavy bar, rats can *easily* push all lighter bars, but if trained upon light bars, they have *difficulty* in pushing heavier bars. The function obtained in the Applezweig study would seem to result primarily from this fact since the data from one-half the *S*s, i.e., those switched to heavier weights during extinction, show resistance to extinction to be a function of increasing amounts of effort required during extinction and of the magnitude of that change in bar weights. The other half, i.e., those switched to lighter weights, showed little or no such relationship.

All the more recent studies attempting to demonstrate the existence of a relationship between lesser amounts of effort and the inhibition of a molar response tendency in bar-pressing situations are open to alternative interpretation because the results are confounded by such uncontrolled variables as number of reinforcements (4, 6), complexity of the task to be learned (1, 3, 4), and delay of reinforcement (4, 7).

One additional factor which may confound a comparison of the effect of different amounts of effort upon resistance to extinction in experiments involving the bar-pressing response (1, 3, 4) is that of the contribution of the operant level of a given bar weight to the measures of resistance to extinction. The lighter weight bar during extinction could allow more for an indiscriminate recording of tangential responses (aggression, operant level, random exploratory behavior) than heavier bars. The interaction of this factor would tend to produce differences in the direction hypothesized by Hull and obtained by other investigators.

The purpose of this study is to determine the relationship between lesser amounts of effort and the resistance to extinction of the molar bar-pressing response while controlling for habit strength, delay of reinforcement, and operant level.

The results of the present study should indicate whether work is a relevant variable in the extinction of a molar response (2, p. 279) and, as a result, suggest the relationship between effort and the accumulation of I_R (2, p. 280).

METHOD

Apparatus. The apparatus employed was a modified Skinner box. The plywood floor, the back, and the removable ¼-in. hardware-cloth cage-like top were painted flat gray. The cage was 12 in. deep, 9½ in. wide at the back, and 13 in. high at the back (inside dimensions). An aluminum bar, approximately ¼ in. thick and ⅜ in. wide, protruded 2 in. into the cage from the center of the plywood back at a height of 3 in. from the floor. The bar could be weighted to require an effort of 5 gm., 40 gm., and 80 gm., and an excursion of ⅝ in. was necessary to activate an automatic feeding mechanism. The food tray was located on the floor, 2 in. to the right of the bar. A standard water tube protruded through the wire screen to the right of the food dish, making water available throughout the entire experiment.

Subjects. Forty-two female albino rats and 12 female hooded rats, 90 to 150 days old, from the colony maintained by the Psychology Animal Laboratory at Michigan State College were used. Thirty albino rats were employed in the main experiment, while 12 albino and 12 hooded rats were used in the subexperiment concerning operant level.

Preliminary training. Untamed *S*s were kept on a reduced diet of 9 gm. of Purina Dog Checkers in their home cages for a period of 5 to 7 days, and on the day prior to the experiment they were individually fed 6 gm. of Checkers. Approximately 23 to 25 hr. later, *S*s were placed in the Skinner box for the major part of the experiment.

To habituate the 30 *S*s used in the main experiment, two Calf Manna pellets weighing approximately 0.05 gm. each were placed in the food tray. This type of pellet was subsequently employed as reward for the bar-pressing response. After eating the pellets, *S*s were manually supplied ten additional pellets by *E* to associate the audible activation of the feeding mechanism with the release of food. Whenever possible, *S*s were allowed to secure pellets unaided. During this phase the bar was weighted to require a 5-gm. effort to activate the feeding mechanism. At the end of the 10 trials, when all *S*s were responding without the aid of *E*, 15 additional free trials were given. The bar-weighting was then shifted to require an effort of 40 gm. to activate the feeding mechanism. All *S*s received 25 additional trials under this condition, being aided on the first two or three trials if necessary. Partial responses, hence partial reinforcement, were eliminated by this procedure. At the end of this preliminary training, all *S*s had achieved a stable though not maximal rate of responding to the bar weighted for a 40-gm. effort.

Throughout the entire experiment, the food-releasing mechanism was activated 1 sec. after the bar was returned to its normal position. This factor was introduced in order to control for any differential delay of reinforcement due to response differences in method of pushing the variously weighted bars.

Experimental design. Following the preliminary training, the weight-loading on the bar was shifted to one of three weights. Ten *S*s were shifted to the 5-gm. loading, ten to an 80-gm. loading, and ten remained on the 40-gm. loading. All *S*s then received 25 reinforcements under their respective conditions. The 80-gm. group was aided for the first two or three trials to effect smooth transition to the new loading. Prior to shifting to the experimental conditions, an effort was made to equate the three groups for response rate, and thus the placement of *S*s into their respective groups was not random in the final stages of the research. Three animals in each group received 25 additional reinforcements, or a total of 50, under their respective conditions prior to extinction, but since no differences were found between these *S*s and the others, their scores were combined for the purpose of statistical analysis. This differential treatment was employed to determine the equivalence of the three habit asymptotes.

Upon completion of this additional training, each group was immediately extinguished under its respective bar loadings by omitting food from the feeding mechanism. Extinction was continued for all *S*s until all measures of extinction were met. These were a 5-min. and a 10-min. no-response criterion, and a 30-min. and a 60-min. period of free responding.

All *S*s were untouched by *E* throughout the entire experiment; preliminary training and extinction were one continual process lasting 2 to 4 hr. All bar depressions were automatically recorded on a constant-speed polygraph located in another part of the room. Temperature, illumination, and extraneous visual stimuli were relatively constant.

The subexperiment concerned the sensitivity of the different bar loadings in recording unlearned and unrewarded bar depressions (operant level). After the deprivation schedule described above, *S* was placed for the first time in the Skinner box for a 30-min. period. No food was present nor were responses rewarded, although the feeding mechanism was activated 1 sec. after bar depression and release. Water was continually present. Operant levels were recorded for three groups employing the three bar weightings used above. Each group was comprised of four albino rats and four hooded rats. Littermates were equally distributed. No noticeable differences between albino and hooded strains or between litters were observed, and the data were combined for statistical analysis.

RESULTS

Habit strength for the three groups prior to extinction was measured in terms of the time required to obtain the last ten rewards in the training period. The mean time required to obtain the last ten rewards was 4 min. 56 sec., 4 min. 57 sec., and 4 min. 42 sec. for the 5-gm., 40-gm., and 80-gm. groups, respectively. Nearly perfect control for this variable was obtained, the *t*'s ranging from .042 to .267 with 18 *df*.

Four criteria were used to determine resistance to extinction. They were: the number of responses obtained during 30 min. and 60 min. of free responding during extinction, and the number of responses to a 5-min. and

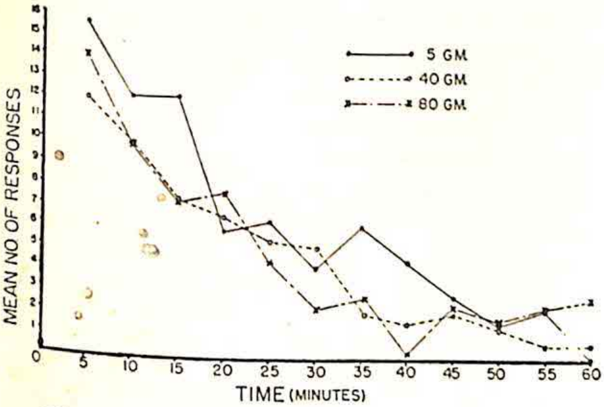

FIG. 1. The influence of effort upon the mean number of responses for successive 5-min. intervals during an hour of continuous extinction

10-min. no-response criterion. Irrespective of the criterion employed, no significant differences were obtained. Inspection of Figure 1 confirms the statistical analysis. It is apparent that amount of work, within the limits employed, bears no relationship to the extinction of a molar bar-pressing response in a free-responding situation when habit strength is controlled.

In the subexperiment concerning the sensitivity of the different bar loadings to the recording of tangential responses, it was found that the 5-gm., 40-gm., and 80-gm. bar weights yielded means of 26.3, 3.88, and 0.75 responses, respectively, during ½ hr. of free responding. The difference in sensitivity between the 5-gm. bar and the 40-gm. bar and the difference between the 5-gm. bar and 80-gm. bar were significant beyond the .01 level of confidence. The *t*'s were 4.73 and 5.53, respectively, with 14 *df*.

The difference between the 40-gm. bar and 80-gm. bar was not statistically significant ($t = 1.99$, 14 *df*). This greater sensitivity of the 5-gm. bar as compared with the 40-gm. bar and 80-gm. bar could account for the slightly greater number of responses made by the 5-gm. group during the first 15 min. of extinction (Fig. 1). When the sensitivity of the bar is not markedly different, as with the 40-gm. and 80-gm. bars, the extinction curves are comparable.

DISCUSSION

The present study indicates that work, within the limits employed, bears no relationship to resistance to extinction, and as a consequence, to the accumulation of I_R (2, p. 279). The data obtained by Mowrer and Jones (4) in a comparable situation may be attributed to the differences in habit strength produced by their preliminary training schedule. Even disregarding the differential rates of responding, which occurred at the outset of extinction in the Mowrer and Jones study, we find that parallel extinction curves ensued. If different amounts of work or energy expenditure do result in differential rates of accumulation of inhibition, then diverging extinction curves should be expected.

The Mowrer and Jones study, far from being convincing evidence of a relationship between work and the accumulation of I_R would seem to support the lack of relationship found in the present study. Even the second part of the Mowrer and Jones study contradicts predictions presumably confirmed in the first part.

Conflicting results of a similar nature were reported by Montgomery (3). When the Applezweig data (1) are broken down into groups that correspond to the present study, i.e., to *S*s extinguished upon the same bar weights that they were trained upon, the results are similar to the results found in the present study.

It is concluded, in light of the present study and available literature, that explanations of extinction phenomena based upon the effects of lesser amounts of work, such as might be encountered in Skinner boxes, T mazes, and other common learning situations, are questionable and contingent upon further research in this area.

SUMMARY

The purpose of this study was to evaluate the effect of differential amounts of work on the resistance to extinction of a molar response. Thirty *S*s were given identical preliminary training in a Skinner-box situation. Three groups were then trained to an equal habit, each being required to depress a weighted bar of 5, 40, or 80 gm., respectively. Extinction trials under the same bar weightings as employed in training followed immediately. Resistance to extinction as a function of the amount of effort was determined by using four different criteria. Analysis of the results showed no relationship between the amount

of effort required to make a response and the resistance to extinction of that response.

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Received May 20, 1953.

PERIODIC REINFORCEMENT INTERVAL AND NUMBER OF PERIODIC REINFORCEMENTS AS PARAMETERS OF RESPONSE STRENGTH[1]

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Reinforcement of an operant generates a potentiality to respond when reinforcement is no longer forthcoming. The number of responses emitted following the cessation of reinforcement is the resistance to extinction of the response (7). One parameter of resistance to extinction is the schedule of reinforcement. A periodic schedule characteristically results in more extinction responses than does regular reinforcement. Operationally the difference between these schedules is this: Under regular reinforcement every occurrence of the response is followed by the reinforcing stimulus. Under periodic reinforcement the first response that occurs after the lapse of a specified interval of time is reinforced. Since Skinner first noted the differences during extinction following these two schedules (10), numerous studies have followed (for a current review of periodic reinforcement, see 5). However, these researches have investigated a limited range of the periodic-reinforcement (PR) interval. J. J. Boren *et al.*,[2] using intervals from .5 to 12 min. and 90 reinforcements, have shown that the function relating resistance to extinction and PR interval has a maximum between 1 and 3 min. This function may be incomplete for two reasons. First, it may have as a parameter that changes its shape the *number* of periodic reinforcements received. Secondly, it does not contain a regular reinforcement group (which may be considered as a group with a zero PR interval). Experiment I of the present study was designed to investigate resistance to extinction as a function of the PR interval over the range of 0 to 6 min. (which encompasses the maximum described above) with two extreme values of numbers of reinforcements.

Skinner (10) has investigated rate of responding as a function of the PR interval. Over the interval range of 3 to 9 min., he found rate to be an inverse linear function of the interval. Experiment I was also designed to permit an analysis of response rate as a function of the PR interval over the range of 0 to 6 min.

In addition, Experiment I would indicate the effect upon extinction-responding of the number of periodic reinforcements; however, the function relating these variables would contain only two extreme points for each interval. Since Williams (11) has shown that the number of regular reinforcements is a parameter of resistance to extinction, it seems reasonable that the number of periodic reinforcements might also be a parameter of resistance to extinction. Experiment II of the present study was designed to investigate resistance to extinction as a function of the number of reinforcements received during training on a single PR interval.

METHOD

Subjects

Male albino rats of Carworth Farms stock were used as *S*s. The animals were 90 to 110 days old when they were received in the laboratory; experimentation commenced 7 to 21 days later. During their stay in the laboratory, they were housed in living-experimental cages described elsewhere (3). Before experimentation they were maintained under ad libitum feeding on a ration composed of Purina Laboratory Chow; during experimentation they were fed the same food, as indicated in *Procedure*. Fresh water was available at all times.

The *S*s were assigned at random to 18 experimental groups of six rats each. Two animals died of respiratory infections; three animals conditioned during regular reinforcement but did not maintain the response during PR. For these reasons the *N*'s of five groups, to be noted, were reduced to five animals.

Apparatus

The experimental room is a lightproof, sound-resistant chamber built within a larger room. The animals were placed here during their experimental sessions; between sessions they were housed in the outside room. There are six identical experimental arrangements that permit training six animals simultaneously. Each arrangement consists of a lever and a food magazine, modified from those described in (3). The lever has been changed to ⅜ in. in diameter to eliminate gnawing behavior encountered with the smaller one. For a bar press to close the microswitch and, hence, to be counted as a response, it must depress the lever approximately 23 mm. with a force of 12 gm. Since slight variations occur from lever to lever, care was taken to see that each animal used the same one throughout its experimental history. To eliminate any systematic group variations as a result of lever differences one animal of each group was trained on each lever. The food magazine now delivers pellets rather than powdered food. These pellets, which are the reinforcing stimuli, are molded from Purina Chow and necessary binding agents into 1-gr. cylindrical forms.[3] Pellets are stored in a brass tube and are delivered into the food chute, one at a time, by the armature on the magazine solenoid.

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[1] Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Faculty of Pure Science, Columbia University. The author wishes to express his gratitude to Prof. F. S. Keller for his constant support and guidance. He is also grateful to Profs. R. F. Hefferline and W. N. Schoenfeld for their interest in, and suggestions concerning, the research.

[2] Boren, J. J. Personal communication, 1952.

The experimental room is ventilated by an exhaust fan operated in conjunction with six outlets from a central compressed air supply. In addition to ventilating the room, this arrangement provides a sound screen that completely masks noises from the controlling apparatus outside. Within the room the sounds of the microswitches and of the magazine solenoids on reinforced responses were audible. A dummy magazine, identical to those in use, was present during PR and extinction and was operated at irregular intervals four times per minute. This magazine was used to eliminate the solenoid sounds as discriminative stimuli for lever pressing.

The controlling apparatus, located in a relay panel in the outer room, consists of a timer and relay circuit that performs the following operations automatically: (*a*) records all responses to the lever, (*b*) after the passage of the appropriate PR interval completes the magazine circuit so that the next bar press produces one pellet, and (*c*) releases the magazine circuit following the reinforcement. The circuit is arranged so that if the bar is already held down when the magazine circuit is completed, it must be released and pressed again before a pellet is delivered. All responses to the lever are recorded on cumulative kymographs and on constant-speed, waxed-tape polygraphs (3) and on electric counters. Reinforcements are recorded on the waxed tapes.

Procedure

The experimental phases were the same for all groups of both experiments except as noted under *PR training*. Experimental sessions for each group were held during the same hour on consecutive days, after establishment of the hunger rhythm. All animals were deprived of food 22 hr. at the beginning of the session and were permitted to eat, without restriction, for 1 hr. following it.

Experimental Phases

Feeding regimen. A procedure of 23-hr. food deprivation followed by 1 hr. of food was carried out for six days to establish the hunger rhythm.

Operant-level determinations. Three daily 40-min. periods of unconditioned bar pressing were given. To facilitate conditioning, 10 min. after the bars had been removed the following operations were performed: day 1, feeding approximately 5 gm. of the regular ration in the pellet tray under the lever; day 2, feeding five pellets, one at a time; and day 3, pairing the magazine sound with 10-pellet deliveries.

Regular reinforcement. To maintain the response during the early stages of PR, the bar-pressing response was conditioned with ten regular reinforcements on the fourth day.

PR training. It has been pointed out (2, 10) that the PR intervals may be timed from each reinforced response or timed by the clock from the beginning of the experimental hour. In actual practice there is little difference between these schedules, and the mean interval between reinforcements, in either case, closely approximates the PR interval. In the present experiments the intervals were timed by the clock. Each experimental session began with a reinforced response and terminated at the end of the PR interval following the last reinforcement. The nature of the problem investigated in Experiment I introduced an uncontrolled variable. If the independent variable is length of the PR interval, it is impossible to control both number of reinforcements and time in the experiment. Lacking experimental evidence, we felt that the number of reinforcements was the more important variable, and this was held constant.

Experiment I, section 1. This involved seven groups of six animals, for which the PR intervals in minutes and the number of reinforcements given per day were 0 (minutes)–40 (reinforcements); ⅙–40; ⅓–40; 1–40; 2–24; 4–12; and 6–10. A total of 240 reinforcements was given each animal.

Experiment I, section 2. This also involved seven groups of six animals. PR intervals were the same as in section 1, but each animal received only 15 reinforcements instead of 240. These were delivered on a single day except for the 6-min. group, which received 8 on the first day and 7 the second. The zero-minute (regular reinforcement) group received only 5 reinforcements in addition to the initial 10 received on the fourth day. An earlier experiment (forthcoming) showed that 20 regular reinforcements prior to 20 reinforcements under 2-min. PR were not reflected in extinction responding when compared with a group receiving only 20 PR. This finding indicates that the extinction responses for those groups in this section receiving 15 *periodic* reinforcements would not be affected by the preceding 10 regular reinforcements. However, Williams (11) has shown a difference between 15 and 25 *regular* reinforcements during subsequent extinction. The findings of these two experiments seem to indicate that a zero-interval group receiving only 5, rather than 15, reinforcements in addition to the initial 10 would permit a more valid comparison with the groups receiving 15 periodic reinforcements.

Experiment II. It was made up of four groups of six animals each. All animals were trained on 2-min. PR; they received different numbers of reinforcements: 50, 85, 120, and 500. Reinforcements were given 25 per day except on the last day for the 85- and 120-reinforcement groups, which received 10 and 20, respectively. Data for 15 and 240 reinforcements were provided by the 2-min. groups of Experiment I.

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[3] An exact assay of the pellets may be obtained from the G. S. Stoddard Co., 123 East 23 Street, New York 10, New York.

Extinction. There were five daily 50-min. periods of extinction, during which the food magazines were disconnected.

RESULTS AND DISCUSSION

The data on unconditioned bar-pressing were collected to determine any initial differences between groups. Each group was compared with every other group in both experiments using the nonparametric Mann-Whitney *U* test (8), and no differences were found. The data were typical of those obtained for the first three days of operant level in this laboratory (4, 9) and are not, therefore, presented.

Experiment I

Over the interval range investigated, response rate does not reach its final stable value until after 80 to 100 reinforcements. For this reason, the data of the 15-reinforcement groups have been omitted from the analysis of response rate. Rate of responding as a function of the PR interval is shown in Figure 1. The points are means of the average rates during the last 35 reinforcements for the 240-reinforcement groups. The differences between the rates for the ⅙-min. group and the remaining ones were tested by the *U* test. All of these differences, except the difference between the ⅙- and ⅓-min. groups, were significant beyond the .05 level of confidence.[4] The curve in Figure 1 has been drawn as a continuous function over the range of intervals greater than zero; however, the rate for the regular reinforcement (zero-interval) group has been plotted to permit a comparison with the other groups. The form of the curve between ⅙ and zero minutes was not determined in this experiment. It seems reasonable to assume, however, that as the PR interval is reduced to an interval equal to or shorter than the eating time, the rate will drop abruptly and will be maintained at a value equal to the rate under regular reinforcement. Over the range of ⅙ to 6 min., the data are in agreement with the finding reported by Skinner (10) that rate of responding is inversely related to interval. It may be seen from Figure 1 that the curve is changing slowly for intervals beyond 3 min. Since Skinner reported a linear function between 3 and 9 min., it is felt that the present data are not in disagreement with his finding. Obviously, a linear function will not describe the curve over its entire range. The data in Figure 1 are of the same form as those reported by Kaplan (6), who investigated intermittent reinforcement of an escape response. His intervals of reinforcement were similar in range to the PR intervals used in the present study.

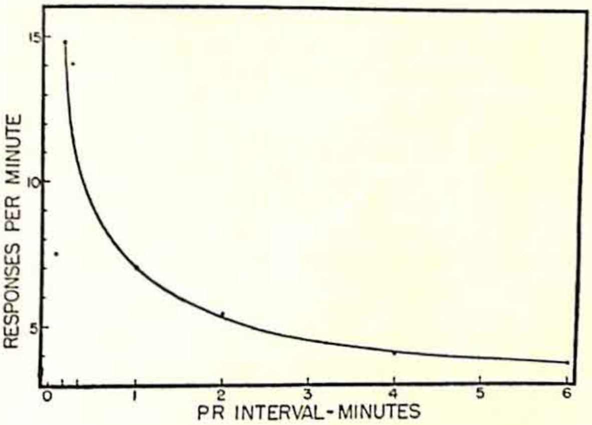

FIG. 1. Mean rate of responding in responses per minute as a function of the PR interval

Mean cumulative response curves for the five days of extinction appear in Figure 2. The curves for the 15-reinforcement groups reflect differential responding during the first hour of extinction. In the remaining 4 hr., the initial differences are maintained; however, during this period the curves are essentially parallel. The *U* test applied to intergroup differences in *daily* extinction responding yielded no significant differences beyond the first hour. A similar analysis was made of the data for the 240-reinforcement groups. In this case, however, different PR intervals resulted in differential responding during the first and the second hours of extinction. Thereafter, there were no significant differences on any given day, although the initial differences were maintained throughout the course of extinction.

The functions relating resistance to extinction and PR interval, obtained by cutting

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[4] The results of these comparisons appear in Document No. 4168, which may be obtained from the American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, ℅ Library of Congress, Washington 25, D. C., by remitting in advance $1.25 for 35-mm. microfilm or $1.25 for 6- by 8-in. photocopies. This document also contains the group statistics for the data in Figures 2 and 4 and the results of applying the *U* test to the intergroup differences of the data in Figure 3. Make checks payable to Chief, Photoduplication Service, Library of Congress.

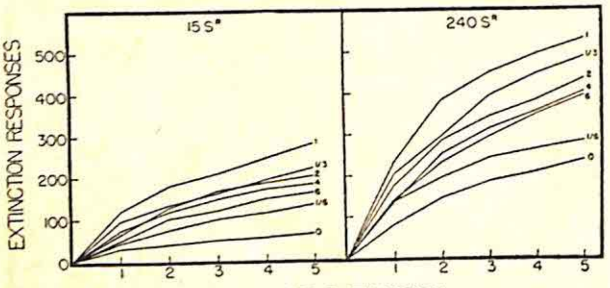

FIG. 2. Mean cumulative response curves during five 50-min. periods of extinction. The parameter of the functions is the PR interval in minutes. Groups received 15 or 240 reinforcements (S^R).

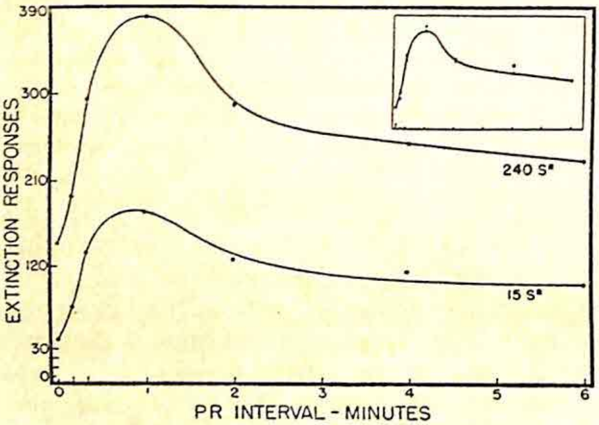

FIG. 3. Mean responses during two 50-min. periods of extinction as a function of the PR interval with number of reinforcements (S^R) as a parameter. Functions were obtained by cutting through the curves in Figure 2 on Day 2. The insert shows the fit of the 15-S^R points (open circles) about the 240-S^R curve when the points of the 15-S^R curve have been multiplied by a constant amount chosen to superimpose the 6-min. interval points.

through the cumulative response curves at any one point, have essentially the same form. As a result of the intergroup comparisons of daily responding, the responses for the 240-reinforcement groups were cumulated over the first two periods of extinction and were plotted in Figure 3. To permit a direct comparison with this function, the data for the 15-reinforcement groups were also cumulated over the first two days of extinction and were plotted in Figure 3, in spite of the fact that these groups did not respond differentially beyond the first hour. It may be seen from Figure 3 that the function relating resistance to extinction and PR interval has a maximum at approximately 1 min., and that the shape of the function is independent of the number of reinforcements. The ratios of corresponding points on the two curves, except for the regular reinforcement groups, are essentially constant. The points in the 15-reinforcement curve have been multiplied by a constant chosen to superimpose the two curves at the 6-min. interval. The fit of these calculated values to the function obtained for the 240-reinforcement groups is shown in the insert in Figure 3. The calculated values (open circles) are sufficiently close to the obtained curve to justify the assertion that the shape of the function is independent of the number of reinforcements. The U test was applied to the data of Figure 3. To determine the differences in extinction following regular and periodic reinforcement, the zero-minute groups were compared with the PR groups receiving the same number of reinforcements. In both curves the differences between regular and periodic reinforcement are significant beyond the .05 level of confidence except for the ⅙- and 6-min. groups receiving 240 reinforcements. The statistical significances of the maxima were determined by comparing the 1-min. group with the remaining groups. Groups that differ significantly (beyond .05) from the 1-min. groups are the 0- and ⅙-min. ones receiving 15 reinforcements and the 0-, ⅙-, ⅓-, and 6-min. ones receiving 240 reinforcements.

The data are in agreement with the findings that periodic reinforcement results in greater resistance to extinction than does regular reinforcement (cf. 5). Compared with the Boren data previously cited, they establish the fact that the function relating resistance to extinction and the PR interval has a maximum that is independent of the number of reinforcements. Boren placed the maximum between 1 and 3 min.; in the present study the maximum is approximately 1 min. In both cases the general location is the same. At the present stage of knowledge it is not possible to state that this shift in the maximum is significant. If it is real, it may result from different experimental arrangements and different levers. Since the position did not change for extreme values of reinforcements given under the same procedure and in the same apparatus, it may be concluded, tentatively, that the position, as well as the existence, of the maximum is independent of the number of reinforcements.

To determine the relation between rate of responding during reinforcement and resistance to extinction, the mean extinction responses for the 240-reinforcement groups in Figure 3 were plotted as a function of the

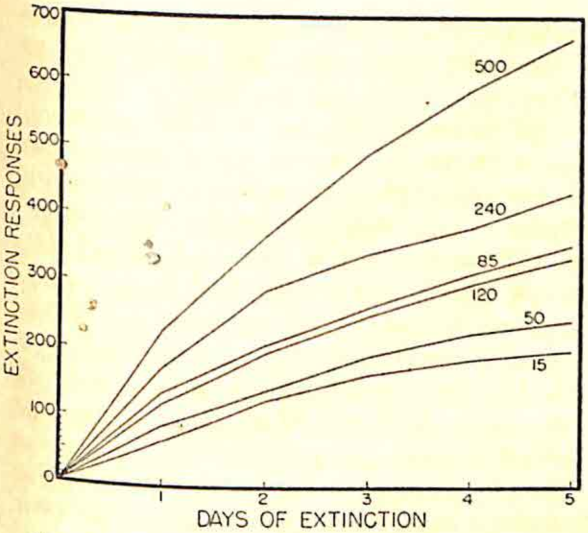

FIG. 4. Mean cumulative response curves during five 50-min. periods of extinction. The parameter of the functions is the number of reinforcements received during 2-min. PR.

mean rates from Figure 1. The plot showed no consistent relation between these two variables. The rates in Figure 1 are mean rates. Since there is some overlap of individual rates in different groups, the animals were regrouped according to their PR rates irrespective of their PR interval, and the mean extinction responses for these new groups were redetermined. Again, a plot of extinction responses versus PR rate indicated no consistent trend in the data. These analyses indicate that resistance to extinction is not systematically related to rate of responding during reinforcement.

Experiment II

The mean cumulative response curves during extinction after different numbers of periodic reinforcements appear in Figure 4. These curves show a marked deceleration in rate during extinction. The 500-reinforcement curve is falling very slowly; the 15- and 50-reinforcement curves are falling much more rapidly. Resistance to extinction has been plotted as a function of the number of periodic reinforcements in Figure 5. Two functions are shown to emphasize the fact that the shape of the curve changes as the extinction period is extended. The lower curve in Figure 5, obtained after 1 hr. of extinction, shows small differences between groups and indicates that the curve is approaching some asymptotic value. The upper curve, obtained after five days of extinction, shows larger intergroup differences and does not suggest any asymptotic value. A linear function has been fitted to these data. It is recognized that the curve does not adequately describe the small reinforcement points, but the data do not suggest any curve that describes them better. The intergroup differences in Figure 5 were compared by the *U* test. The results of these comparisons appear in Table 1.

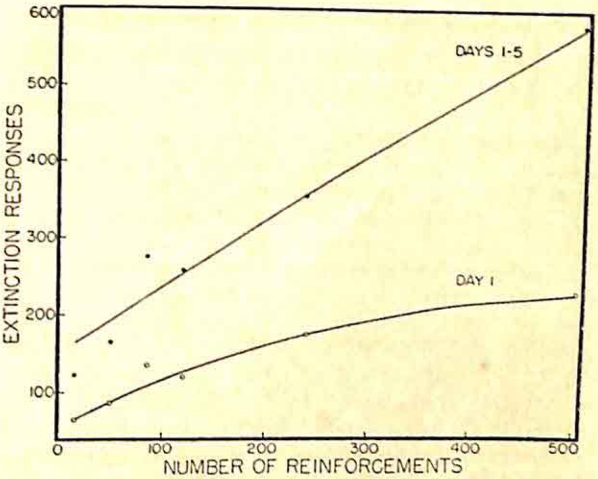

FIG. 5. Number of extinction responses as a function of the number of reinforcements received during 2-min. PR. The lower curve was obtained by cutting through the cumulative curves in Figure 4 on Day 1, the upper one by cutting through on Day 5. The points on the upper curve have been lowered 80 responses along the ordinate.

TABLE 1

Reliabilities of Intergroup Differences in Extinction Responding Determined by the Mann-Whitney *U* Test

Numbers in the frame of the table refer to number of reinforcements during 2-min. PR. Probabilities appear in the body of the table.

EXTINCTION DAY 1

	50	85	120	240	500
15	.531	.032	.013	.047	.001
50		.047	.021	.047	.021
85			.409	.197	.294
120				.120	.066
240					.409

EXTINCTION DAYS 1 THROUGH 5

	50	85	120	240	500
15	.469	.047	.066	.120	.001
50		.090	.090	.120	.008
85			.469	.350	.090
120				.294	.066
240					.066

An inversion between the 85- and the 120-reinforcement groups cannot be accounted for in terms of the experimental operations. The differences between these groups on any one day during extinction or on any cumulated days is not significant. This indicates that the inversion may be due to random fluctuations and is not, in fact, a real inversion.

The Bush and Mosteller learning model (1) presents rational expressions for the relations obtained in this study. Figure 1 should be described by their equation 37; Figure 5 by equation 20 or, if the number of reinforcements has not been sufficient to generate the final rate under reinforcement, by equation 23; Figure 3 by combining equations 37 and 20; and the relation between rate under reinforcement and extinction responses, which, in the present study, were found not to be systematically related, by equation 20. The application of the model to functions containing PR interval as a parameter is difficult because of the dependence of the "constants" ω and b on T, the PR interval. Since the explicit relations between these variables are not given, a rigorous test of the adequacy of the model to describe the present data is not possible. It might be pointed out that equation 37 does describe the data in Figure 1, but only if ω and b are assumed to be constants independent of T. If this assumption is made, the authors have pointed out that the model cannot handle the differences in extinction following regular and periodic reinforcement.

SUMMARY

The male albino rat, on a hunger rhythm, was used in a Skinner-type apparatus to study the effects of the periodic-reinforcement interval and the number of periodic reinforcements upon response strength.

In Experiment I, periodic-reinforcement intervals of 0 (regular reinforcement), ⅙, ⅓, 1, 2, 4, and 6 min. were used to condition the bar-pressing response. Two values of the parameter of number of reinforcements, 15 and 240, were presented at each interval.

1. The function relating rate of responding and the periodic-reinforcement interval shows an inverse relationship between these variables over the interval range from ⅙ to 6 min. It is argued that as the interval is decreased to a value equal to the eating time, the rate will drop abruptly to the value maintained under regular reinforcement.

2. The function relating resistance to extinction and the periodic-reinforcement interval has a maximum at approximately 1 min. The shape of the function and the position of the maximum appear to be independent of the number of reinforcements.

3. There appeared to be no systematic relation between rate of responding under periodic reinforcement and resistance to extinction.

In Experiment II resistance to extinction was investigated as a function of the number of reinforcements received under 2-min. periodic reinforcement. Numbers of reinforcements used were 15, 50, 85, 120, 240, and 500. As the number of reinforcements increases, resistance to extinction increases. The exact form of the relationship is not indicated from the data. The effect of the variable number of reinforcements may be obscured if the extinction period is truncated.

The limitations of the Bush and Mosteller learning model in describing functions containing periodic-reinforcement interval as a parameter are indicated.

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Received May 9, 1953.

TEMPORAL FACTORS IN SENSORY PRECONDITIONING[1]

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This experiment is derived from an interpretation of sensory preconditioning (2) in terms of mediated stimulus equivalence (5). The presentation of paired preconditioning stimuli is likened to classical conditioning. Each stimulus is considered to be a UCS for a response that is not directly observed, and potentially a CS for a second response similar to the one elicited by the other stimulus. Prior to preconditioning, both responses occur only if both stimuli are present. After preconditioning, a response which resembles the entire complex follows presentation of either stimulus.

If an instrumental response is subsequently conditioned to one of these stimuli, several invariant stimuli are present in the situation. These include the stimulus itself, stimuli derived from its UCR, and stimuli derived from its CR. Since the latter stimuli are presumably similar to those produced by the UCR to the other preconditioning stimulus, the presentation of this stimulus in critical tests should be expected to yield positive transfer.

A prediction can be deduced to test this argument from laws of temporal relations in conditioning (4, 6). Since a CR is most readily established if the CS precedes the UCS, asynchronous forward presentation of the preconditioning stimuli should facilitate acquisition of the mediating CR. The amount of transfer should be correspondingly greater than that obtained after simultaneous or backward presentation.

METHOD

Subjects

The 120 hooded and albino rats employed in this experiment were assigned at random to the various treatments. Animals of both sexes were used, and ages ranged from 50 to 125 days.

Preconditioning Apparatus

Preliminary exposures to single or paired stimuli took place inside a partially sound-shielded room. A cage of wire mesh secured to an enamel pan filled with sawdust and placed upon a table was provided for the animals. Light from a 100-w. incandescent lamp in a ceiling fixture served as one of the two preconditioning stimuli. The other was produced by a buzzer which was located about 2 ft. from the cage. Switches in the lamp and buzzer circuits were operated by an automatic timing device.

Conditioning Apparatus

After preliminary training, the animals were conditioned in a box 16 in. square inside, 5 in. high, with an electric grid at its base. The box was covered by a sheet of plate glass with an opening in its center. A transparent plastic container rested on the grid floor and protruded 3 in. through the opening. A 60-w. incandescent lamp was mounted, base up, inside the container, and a buzzer was attached to its top. A motor-driven kymograph drum, which activated microswitches, was used for automatic presentation of the stimuli at a rate of two per minute. A shocking circuit for the grid was devised from a 110-v. a.c. supply and a series of resistances.

Procedure

The animals were divided into six main groups, three control and three experimental. Animals assigned to the first control group received no preliminary training, but were transported directly from their home cages to the conditioning apparatus. Animals in the second control group were exposed to a pseudoconditioning series of 3000 buzzer presentations during a period of 4 hr. 20 min. The third group was another pseudoconditioning control, but a light was presented instead of a buzz. Each stimulus lasted for 1 sec. The control groups were subsequently divided into subgroups of ten animals each. Half the rats were trained to run when a light was presented and then tested for transfer to buzz, while half were first conditioned to buzz and then tested for transfer to light.

Rats assigned to the first experimental group were given preliminary training which consisted of 3000 simultaneous presentations of buzz and light. This is *simultaneous preconditioning*. Half the rats so treated were then conditioned to run to light and tested for transfer to buzz, and half were conditioned initially to buzz and tested for transfer to light.

During the preconditioning session half the animals of the second experimental group were exposed to light followed by buzz. These rats were then conditioned to

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[1] This article is based upon a thesis submitted by the senior author to the Graduate School of The Ohio State University in partial fulfillment of the requirements for the degree of Master of Arts.

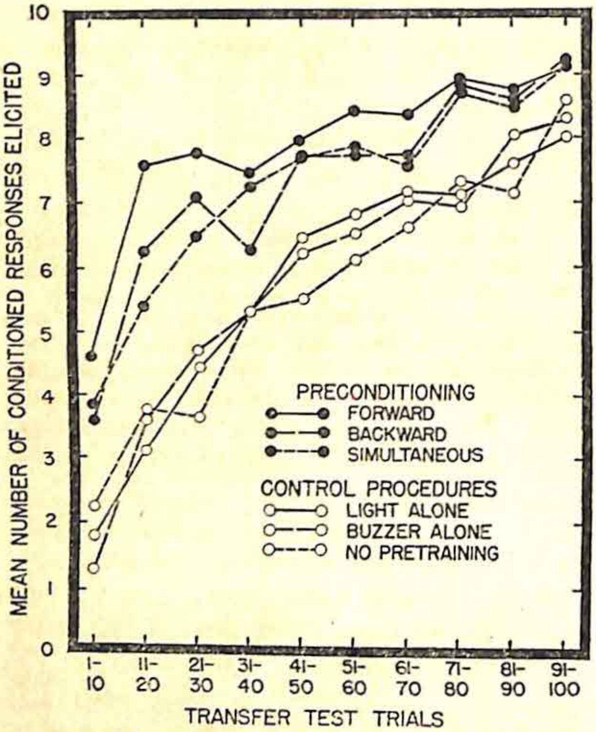

FIG. 1. Learning curves for acquisition of the CR to the transfer stimulus

TABLE 1

Analysis of Variance for Number of CR's Elicited in Transfer Task

SOURCE	df	EST. MEAN SQUARE	F	p
Between conditions	5	1845.71	27.93	<.01
Between subgroups	1	42.01	<1	N.S.
Interaction	5	36.97	<1	N.S.
Within subgroups	108	66.08		

run to buzz and tested for transfer to light. The remaining animals were first exposed to buzz followed by light, and then were conditioned to light and tested for transfer to buzz. This is *forward preconditioning*, for the UCS for the mediating response follows the stimulus that is to become the CS.

These temporal relations were reversed for the treatments given to the third experimental group. Animals exposed to light-buzz sequences were conditioned to light and tested for transfer to buzz. Those given presentations of buzz-light were conditioned to buzz and tested for transfer to light. This is *backward preconditioning*. Under both conditions of asynchronous preconditioning a ½-sec. interval elapsed between stimuli of 1-sec. duration. There was thus a 1½-sec. interval between onsets. This seems long, but is justified by Kappauf and Schlosberg's results (3).

In the conditioning procedure each CS lasted 1 sec. A CR was defined as a movement of at least 6 in. prior to onset of shock, which followed by ½ sec. the termination of the CS. One rat was discarded because it failed to respond to shock within a 10-sec. period. The criterion for conditioning was 7 responses within a block of 10 trials. The transfer tests which followed immediately consisted of stimulus substitution for 100 additional trials.

RESULTS

The first statistical tests were performed to ascertain the effects of the different conditions upon the number of trials required to reach the initial criterion in conditioning. The 12 subgroups were treated separately. After initial tests indicated homogeneity, a within- and between-groups analysis of variance was performed. An $F < 1$, with 11 and 108 *df*, was obtained. This is in accord with previous findings (2) that preconditioning procedures have no demonstrable effect upon initial conditioning.

The most extensive analysis was performed upon the total number of CR's elicited during transfer tests. Figure 1 shows the learning curves obtained in the transfer situation after varying conditions of pretraining. The scores were tested for homogeneity, and the assumption was not rejected. The analysis of variance summarized in Table 1 was then performed. It was found that amount of transfer differed significantly from subgroup to subgroup, and that these effects could be attributed to differences in pretraining.

Subgroups within conditions were then combined, and an analysis of variance was performed to compare control treatments. An $F < 1$ was obtained, with 2 and 57 *df*, obviously not significant. A similar analysis compared the three experimental groups: forward, backward, and simultaneous preconditioning. This yielded an F of 8.01, which is significant beyond the .01 level with 2 and 57 *df*.

A series of t tests revealed that backward and simultaneous preconditioning groups were not statistically distinguishable, but that forward preconditioning yielded significantly more transfer than either of the other treatments. The values were 0.11 for backward vs. simultaneous, 3.46 for backward vs. forward, and 3.11 for simultaneous vs. forward comparisons. The latter two are significant beyond the .01 level of confidence. A final t of 6.73, significant at the .01 level, was obtained in a comparison of the pooled control groups and the pooled backward and simultaneous preconditioning groups.

DISCUSSION

The results of this experiment demonstrate transfer from preconditioning to an extent that cannot be attributed to pseudoconditioning. Furthermore, the temporal relations between preconditioning stimuli affect the amount of transfer that is obtained. Since forward presentation is superior to either backward or simultaneous presentation, the data confirm the hypothesis under test. Although the postulated mediating CR remains obscure, conditions designed to facilitate its fixation yield increments of the kind to be expected.

The prediction supported by this investigation has been derived from an S–R analysis. It is not contended that the outcome is antithetical to an S–S point of view (1), but rather that preconditioning cannot be offered in exclusive support of the latter position. The critical tests to distinguish between these alternatives might be profitably sought elsewhere, for it is unlikely that sensory preconditioning will provide a stumbling block for either.

SUMMARY

This experiment was designed to test the hypothesis that transfer in preconditioning experiments varies in amount as a function of the temporal relations between preconditioning stimuli. This is predicted by accounts which postulate response mediation and liken the preconditioning procedure to classical conditioning. Six main conditions were employed, with 20 rats in each group. The procedures were forward, backward, and simultaneous preconditioning; light and buzzer pseudoconditioning; and no-pretraining control. After *S*s were given preliminary training they were conditioned to run upon presentation of either light or buzzer. Subsequently, transfer to the alternate stimulus was measured in a standard block of conditioning trials.

It was found that groups which received pseudoconditioning presentations could not be distinguished from the one given no pretraining. Transfer was observed if rats were given any of the preconditioning treatments, and of the three the forward preconditioning groups showed the greatest amount of transfer. It was concluded that an S–R analysis gives a satisfactory account for these findings, and that the data from sensory preconditioning experiments cannot be offered in exclusive support of S–S theories of learning.

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Received March 29, 1953.

THE ROLE OF THE EXPLORATORY DRIVE IN LEARNING

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In previous papers the author has presented evidence that novel external stimulation evokes the exploratory drive which leads to exploratory behavior, that continued exposure to such stimulation results in a decrease in the strength of the exploratory drive, and that the exploratory drive is a primary drive largely independent of other primary motives (5, 6, 7).

The present investigation is concerned with the role of the exploratory drive, as a primary drive, in learning. According to drive-reduction theory, behavior followed by a reduction in amount of exploratory drive should be strengthened. However, qualitative observation by the author has repeatedly suggested an alternative hypothesis: behavior which results in an *increase* in amount of exploratory drive is strengthened. In other words, it is possible that behavior which produces novel stimulation is reinforced, not because exposure to that stimulation reduces the strength of the exploratory drive, but because the novel stimulation produces an increase in, or at least maintains, the strength of the exploratory drive. Results reported by Mote and Finger (4), by Schiller (9), and, in particular, by Harlow *et al.* (1, 2) tend to support the latter hypothesis.

The present experiment is designed (*a*) to test the hypothesis that novel stimulation can function as a reinforcing agent, and (*b*) to provide evidence relevant to the question of whether exploratory-drive reduction or exploratory-drive increase (or maintenance) is the mechanism underlying this kind of reinforcement.

The experimental conditions had to meet two major requirements. First, drives other than the exploratory drive and reinforcements other than those provided by novel stimulation had to be eliminated or controlled. Second, a situation had to be devised in which the exploratory drive could be evoked and then either reduced or increased (maintained) in strength after a response had occurred. These requirements were met by running rats satiated for food and water, with a control for the activity drive, in a Y maze so constructed that one arm was a blind alley and the other opened into a large Dashiell-type maze offering a much greater amount of intra- and extramaze stimulation. On any given trial an animal was free to enter either arm of the Y; as soon as it did so, a sliding door was closed behind it, and approximately 2 min. later it was removed from the maze.

Thus, the situation (*a*) provides an opportunity for learning to occur, and (*b*) permits of a rough test between the exploratory-drive reduction and the exploratory-drive increase hypotheses. According to the former, the animals should learn to enter the blind alley of the Y because continued exposure to that arm produces an appreciable decrease in the strength of the exploratory drive it evokes originally (5). According to the latter hypothesis, the animals should learn to enter the arm leading to the Dashiell maze because it provides a large amount of novel stimulation which increases, or at the very least maintains, the strength of the exploratory drive evoked by the Y-maze arm. An additional test for learning consisted of reversing the Dashiell maze from one arm of the Y to the other midway through the experiment. Preferences developed for either arm of the Y maze should shift accordingly if they are under the control of either of the above two kinds of reinforcement.

METHOD

Subjects

The *S*s were 12 female albino rats of the Wistar strain, averaging about 150 days of age at the beginning of the experiment.

Apparatus

A diagram of the apparatus is presented in Figure 1. It consisted of two mazes, a Y maze with L-shaped goal arms and a modified Dashiell maze (D maze) which could be attached to either arm of the Y. The L-shaped arms prevented the animals from seeing the position of the D maze from the choice point of the Y. The mazes were set on a table placed in the center of the experimental room in which the rats were housed. Dim indirect lighting was used during the experimental periods to provide uniform illumination in the apparatus.

Procedure

Housing and adaptation. On day 1 the animals were placed in the experimental room. Half were housed on the right side of the room and half on the left. Half the rats on each side of the room were housed in small individual cages and the other half in small individual cages attached to activity drums. Throughout the experiment food and water were always available in the living cages. Daily records were taken of number of activity-wheel revolutions. The animals were given 24 hr. to adapt to the experimental room. All had been thoroughly tamed prior to day 1.

Test for turn or position preferences. On day 2 each animal was given four widely spaced, free-choice trials in the Y maze, whose arms were made into blind alleys. As soon as the rat entered an arm, the sliding door was closed behind it. It was removed from the maze 30 sec. after entering an arm. The arm entered and the latency of entry were recorded for each trial.

Learning series. On days 3, 4, and 5 each animal was given eight trials in blocks of four. The D maze was attached to the right side of the Y maze for half the animals and to the left side for the other half. A trial consisted of (*a*) placing a rat in the stem of the Y, (*b*) permitting it to enter either arm, (*c*) closing the sliding door behind it, and (*d*) removing it from the apparatus 2 min. after it was placed in the stem of the Y. The intertrial interval within each block of four trials varied from about 15 to 25 sec.; the interblock interval averaged about 1 hr. On each trial a record was made of the arm of the Y maze entered, the latency of entry, and the number of 12-in. units traversed in the D maze when the animal entered that arm of the Y.

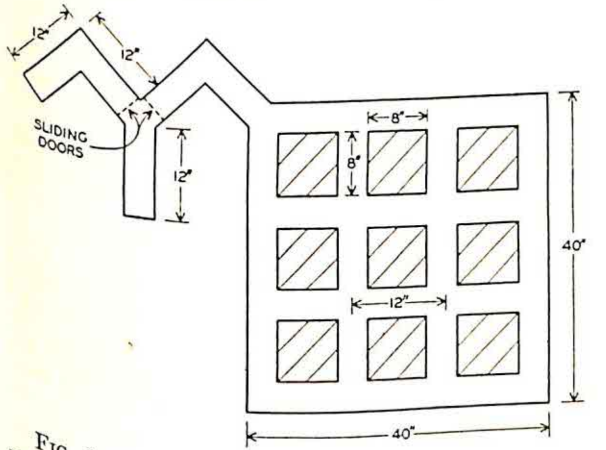

FIG. 1. Floor plan of the apparatus. The measurements shown are inside dimensions. All alleys were 4 in. wide and 5 in. high, and were covered with hardware cloth. The walls and floor of the Y maze and the outside walls of the D maze were constructed from unpainted ½-in. plywood; the floor and the inside walls of the D maze were made from unpainted Homosote (a wall board).

Reversal series. On days 6, 7, and 8 the procedure followed during the learning series was duplicated in all details. The only change in the situation was that the D maze was moved to the other arm of the Y maze.

Experimental Design

The experimental design was such that the following variables were balanced: the type of living cage, the side of the room on which the living cage was placed, and the side of the Y maze on which the D maze was placed during the learning (and reversal) series. All possible combinations of these three variables were used, resulting in eight subgroups of animals. Four subgroups contained two animals each, and the other four contained one rat each. The 12 animals were so assigned that half of them contributed to each of the two "values" of each of the three variables.

RESULTS

Percentage Choice of the D-Maze Side of the Y Maze

For each animal the total number of entries of the Y arm leading to the D maze was tabulated for each block of eight trials during the learning and reversal series. These values were summed for the 12 animals and converted to percentages. The results are summarized in the upper half of Figure 2. The first point represents the percentage choice of the right arm of the Y on the four initial-preference trials. The horizontal lines at 63 and 37 per cent represent the .01 fiducial limits based upon chance.

Inspection of the graph reveals that the animals (*a*) learned to enter the arm of the Y leading to the D maze and (*b*) reversed their behavior when the position of the D maze was reversed. Individual records are consistent with the performance of the group.

Latency Data

The mean latency for the group was computed for the four initial-preference trials and for each succeeding block of eight trials. Also, the common logarithm of each rat's latency on each trial was obtained, and averages corresponding to the latency means were computed. The results are summarized in the lower half of Figure 2. Both curves resemble typical learning curves. The decreases in mean log latency from the first to the fourth and from the first to the seventh point on the graph are highly significant. The respective values of *t* are 5.11 and 7.00; for 11 *df* both values are significant at beyond the .001 level.

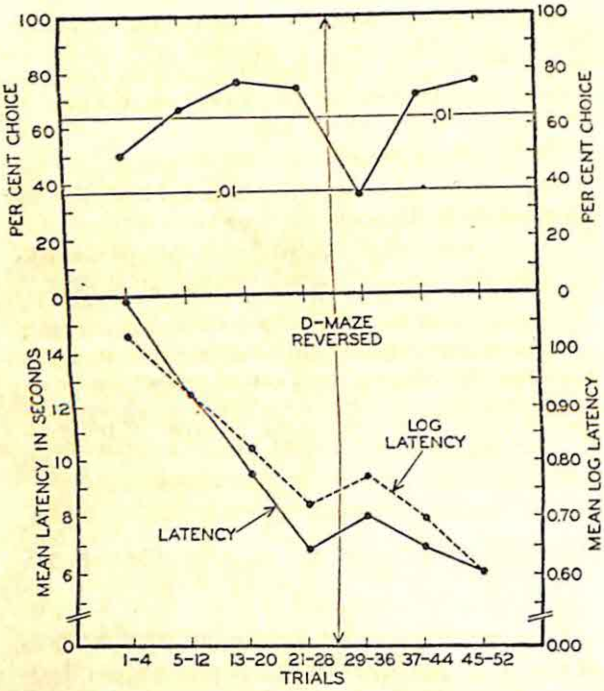

FIG. 2. Group learning curves

Reversing the position of the D maze produced an apparent temporary increase in the latency measures. However, the increase in mean log latency from trials 21 to 28 to trials 29 to 36 does not differ from zero (*t* of 1.01; 11 *df*).

Further Analyses

On the four initial-preference trials six animals turned either left or right three times; each of the other six rats turned left twice and right twice. There were no differences in performance between these two groups during either the learning or the reversal series.

During the learning series the D maze was attached to the right arm of the Y for half the animals and the left arm for the other half. There were no differences in performance between these two groups. Similarly, these groups did not differ during the reversal series.

It is possible that extramaze stimuli deriving from the side of the room on which the animals lived evoked an acquired drive, or provided secondary reinforcement, for entering the arm of the Y pointing toward that side of the room. Hence, learning would be either facilitated or hindered, depending upon the relative position of the D maze. The results yield no evidence of such effects.

No differences in performance occurred between the six animals given access to activity drums and the six not given such access. During the learning series the former group entered the Y arm leading to the D maze a total of 108 times and the latter group a total of 101 times. Corresponding totals for the reversal series are 74 and 63. Furthermore, these groups did not differ significantly in amount of activity in the D maze. The average number of 12-in. D-maze units traversed per D-maze entry was 28.1 for the activity-drum group and 24.8 for the other group. On the average the animals in the former group ran about one-third mile per day in the activity drums.

A progressive increase in amount of D-maze activity occurred during the experiment. The mean number of 12-in. D-maze units traversed per D-maze entry was computed for each block of eight trials during the learning and reversal series. These values are 19.5, 24.2, 26.6, 30.6, 29.4, and 30.3. The difference between the first and last mean is significant at the .001 level (*t* of 5.84; 11 *df*).

DISCUSSION

Both the percentage choice and the latency data indicate that learning occurred. During the learning series the animals developed a preference for the arm of the Y leading to the D maze, and during the reversal series they reversed this preference; average latency decreased systematically as a function of number of trials. Various analyses reveal that performance was not influenced by initial turn or position preferences, by drives or reinforcements acquired in the experimental room, or by the placement of the D maze relative to the Y maze. Moreover, there is no evidence that the general activity drive affected performance in any way.

Thus the results appear to confirm the hypothesis that novel stimulation can function as a reinforcing agent. However, there are three other possible explanations of the present findings that must be considered. Because all the rats were females, it is possible that an activity drive based upon the estrus cycle was present and that the D maze provided a means of partially reducing this drive, thus influencing the Y-maze choices. There is, however, no evidence in the present results of any kind of systematic variation either in amount of D-maze activity or in the latency measures such as would be expected if this motive were important.

Another possible explanation is that a conditioned fear of the blind alley developed because the animals were picked up every time they entered it; hence, they tended to avoid the blind alley and to enter the other arm. There are at least two reasons why this hypothesis is untenable. First, because the arms of the Y were very similar, fear conditioned to one arm should generalize to the other. Thus the animals should tend to avoid both arms, and their average latency should increase with number of trials. Figure 2 shows that mean latency decreased during the experiment. Second, when the rats entered the Y arm leading to the D maze they were almost always picked up in the D maze. If handling results in fear conditioning, then the animals should exhibit an increasing avoidance of the D maze, i.e., a progressive decrease in amount of D-maze activity as number of trials increases. The results show that a progressive increase occurred.

Finally, it is possible that the D maze provided some kind of secondary reinforcement based upon learning that occurred *prior* to the experiment. Available evidence (e.g., 8) indicates that for the rat the secondary reinforcing properties of stimuli extinguish rapidly if primary reinforcement is withheld. Hence one would predict an initial increase followed by a decrease in percentage choice of the Y arm leading to the D maze and an initial decrease followed by an increase in the latency measures. The data presented in Figure 2 contradict both predictions. The preceding considerations apply to secondary reinforcement derived from positive primary reinforcers, e.g., food and water. Miller (3) has demonstrated that secondary reinforcement based upon reduction of an acquired fear drive is effective over a long series of trials. Thus, the present results might be explained by assuming that the Y maze evoked an acquired fear drive, based upon prior learning, that was reduced only when the animals entered the D maze. Qualitative observation yielded no evidence supporting this hypothesis. Only one or two rats defecated or urinated in the stem of the Y, and all the animals ran back and forth between the Y and D mazes freely when they entered the Y arm leading to the D maze.

It is concluded that the present results support the hypothesis that novel stimulation can function as a reinforcing agent. The results are also interpreted as supporting the hypothesis that the mechanism underlying this kind of reinforcement is an increase in the strength of the exploratory drive, and as providing negative evidence for the hypothesis that the mechanism is a decrease in the strength of the exploratory drive.

SUMMARY

Two hypotheses are tested in the present experiment: (*a*) novel stimulation can function as a reinforcing agent, and (*b*) the mechanism underlying this kind of reinforcement is an *increase*, rather than a decrease, in the strength of the exploratory drive. Twelve rats were given 48 free-choice trials in a Y maze in which one arm led to a blind alley and the other to a large Dashiell-type maze. On the first 24 trials the D maze was attached to one arm of the Y; on the second 24 trials it was moved to the other arm of the Y. The results show (*a*) that during the first 24 trials the animals learned to enter the arm of the Y leading to the D maze and that they reversed their choices during the second 24 trials, and (*b*) that over the 48 trials the animals exhibited a progressive decrease in latency of Y-maze–arm entries. It is concluded that learning occurred, that it is based upon the exploratory drive, and that the results support both the above hypotheses.

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Received May 8, 1953.

TRAUMATIC AVOIDANCE LEARNING: THE EFFECTS OF CS–US INTERVAL WITH A TRACE-CONDITIONING PROCEDURE[1]

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Though avoidance learning poses critical problems for S-R theories of learning, parametric studies of avoidance are notably few in number. Particularly, the effects of varying the time interval between the conditioned and the unconditioned stimulus are not well known. The early study by Warner (15) indicated that rats require more trials to achieve an avoidance criterion as CS-US interval is lengthened. The rats, however, had been pretrained to escape shock. There was no study of extinction, and many characteristics of acquisition were not reported. The present experiment explores the effects of CS-US interval on the acquisition and extinction of a shuttle-box avoidance response by dogs.

METHOD

Subjects and Apparatus

The *S*s were 50 experimentally naive mongrel dogs. They ranged in age from about one to six years, and in weight from about 9 to 13 kg. The animals were housed in laboratory cages, with food and water freely available at all times. The data were obtained while the dogs were in apparent good health.

The apparatus used was much the same as that described by Solomon and Wynne (14). The shuttle box consisted of two identically built compartments, separated by a barrier which was adjustable in height. There was *no* drop-gate to prevent retracing. Thus, the dogs were always free to jump from one compartment to the other. The inside dimensions of each compartment were: length 45 in., width 24 in., height 40 in. The plywood walls were sheathed on the inner surface by aluminum painted a flat black. The barrier between compartments was built of aluminum-sheathed plywood slats slipped one on top of another. The compartments had hinged doors which could be locked by slide bolts. The ceiling was composed of hardware cloth. There were two 40-w. lights above each compartment, and two layers of cheesecloth were draped over scaffolding above the apparatus to serve as a crude one-way screen for *E*.

The floor of the apparatus consisted of 1-in. stainless steel bars ½ in. apart. The grid bars were individually wired to a commutator. The method of construction (14) made certain that the dog could not escape shock by short-circuiting adjacent bars with feces or urine. The shock circuit was powered by a 500-v. a.c. transformer energized by 110 v. a.c., with a fixed resistance of 3500 ohms placed in series with the grid bars. The voltage at its source could be varied from 0 to 500 v. Throughout the experiment, the voltage used was the *highest possible* without producing tetany of the dog's leg muscles. The voltage applied to the circuit thus differed somewhat from dog to dog and from day to day. The current drawn at a just-subtetanizing stimulation level (the US) was about 10.0 to 12.5 ma. for most dogs.

To serve as CS, a damped house buzzer was mounted on each end of the apparatus. The two buzzers had been adjusted for equal pitch and volume. The presence of the buzzers, and the fact that passage between the compartments is never blocked by a drop-gate, constitute the only differences between the present apparatus and the Solomon and Wynne shuttle box.

Design

The experimental design provides a straightforward test for the effects of the CS-US parameter. There were four experimental groups, with ten animals in each group. The groups were treated alike in every way except for the length of CS-US interval. The dogs were assigned at random to experimental groups, and the breakdown of each group in terms of sex, age, and size is similar. The CS-US interval was constant for a given dog, but different groups were trained with intervals of 5, 10, 20, and 40 sec. between CS and US. The CS-US interval was measured from the onset of the CS to the onset of the US. There were also two sensitization control groups, with five dogs in each group. These animals were exposed both to the US and to the CS, but never to the CS and US paired.

Procedure

Acquisition. The barrier between the two compartments was set at the height of the dog's back, and the animal was coaxed into the apparatus. The first 10 min. in the apparatus served as a pretest for the "operant level" of barrier-jumping; *E* did nothing during this period but observe the dog's behavior. The 50 animals employed in the study all failed to jump over the barrier during the 10-min. pretest. Five dogs which did jump during the pretest were discarded.

The CS was first presented after 10 min. The CS was the sounding *for 2 sec.* of the buzzer on the side where the animal stood. Then, at the appropriate interval following onset of the CS, the grid of the side where the dog stood was charged (US). The short duration of the CS, it should be noted, constituted a *trace*-conditioning procedure. The shock was kept on until the animal jumped over the barrier into the opposite compartment. The interval between trials was set at a fixed, irregular schedule for all dogs. The intertrial intervals were 2, 3, and 4 min., with a mean of 3 min.

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[1] This paper is based upon a Harvard Ph.D. thesis. The study was supported by funds from the Medical Sciences Division of the Rockefeller Foundation and was facilitated by the Laboratory of Social Relations, Harvard University. It was carried out with the aid and advice of Professor Richard L. Solomon.

When a dog jumped over the barrier after the onset of the CS and before the scheduled onset of the US, shock was omitted for that trial. The avoidance of shock was effected by a single jump; even if the dog immediately jumped back into the compartment in which it began the trial, no shock was given for the retrace. Trials on which the dog jumped the barrier after the CS without being shocked are termed "avoidances"; trials on which the dog terminated shock by jumping are termed "escapes." The training trials, each ending either in escape or avoidance, were continued in one experimental session until the dog had achieved an acquisition criterion of five consecutive avoidances.

Extinction. Three minutes after the dog's fifth consecutive avoidance, extinction trials were begun. The CS was still presented at the same intertrial intervals, but the US was never again applied. Ten extinction trials were conducted on the first experimental day. They were followed by a 5-min. "cooling-off" period for the dog. The dog was then returned to its home cage. The second, and all succeeding, experimental days followed the pattern of the first day's extinction trials. The 10-min. observation period was followed by ten CS presentations and by a 5-min. cooling-off period. Thus, each daily extinction session lasted 42 min. The extinction trials were continued until the dog had achieved an extinction criterion of five consecutive failures to respond to the CS by jumping. However, if extinction had not occurred within ten days (100 trials), the animal was discontinued.

Control group procedure. The control animals were given a number of shocks *without any CS*, spaced at the same intertrial intervals employed with the experimental groups. The shocks were terminated when the animal jumped to the opposite compartment. The "acquisition" period consisted of 7 shocks for five control dogs, and of 17 shocks for five other control dogs. Then, for ten trials a day for ten days, the *CS alone* was presented. These trials corresponded to the extinction trials given to the experimental animals. Thus, any tendency to jump resulting from sensitization or pseudoconditioning should be reflected in the behavior of the control dogs.

Measures

The latency of the jumping response for each trial was recorded by stop watch to the nearest .10 sec. The latency data reveal whether a given trial was an escape or avoidance. During extinction, if no jump occurred within 30 sec. after the CS, the latency was arbitrarily defined as "infinite," and the dog was charged with a failure to respond to the CS.

The frequency of "spontaneous jumping" was also recorded. Whenever *more than one* jump occurred between two presentations of the CS, all jumps following the first were scored as spontaneous jumps. Whenever, during extinction, the first jump occurred more than 30 sec. after the CS, it, too, was scored as a spontaneous jump. Finally, jumps occurring during the observation and cooling-off periods were also scored as spontaneous.

There was also a rough, qualitative observation by *E* of the animals' overt "emotional" behavior. Protocol notes were kept concerning locomotion, barking, trembling, panting, defecation, urination, vomiting, etc. The bulk of this material is not in quantitative form.

RESULTS[2]

Acquisition

The most obvious index of acquisition of the avoidance response is provided by the number of trials required for the dog to reach the acquisition criterion. This is given in Table 1, which lists the mean and median trials on which the *last shock* occurred for each group.

Table 1, it will be noted, presents data for the 40-sec. group under three separate headings. This split was necessitated by a peculiarity observed during the training of these dogs. Very early in training, six of the ten dogs in this group developed a phenomenal rate of "spontaneous jumping." These animals, regardless of the presentation of the CS, were jumping across the barrier as many as 18 times per minute! This rate of spontaneous jumping, as will be seen, was far above that observed in other groups. The prolonged burst of spontaneous jumping, if it extended beyond 15 min., was enough to "pass" the acquisition criterion. That is, a jump would occur within 40 sec. after the CS five times in succession. These jumps, however, *did not appear to be elicited by the CS*. The dogs in question promptly "extinguished" as soon as the spontaneous jumping burst came to an end. They then showed no evident reaction to the CS. These animals thus appear to have achieved the acquisition criterion *spuriously*.[3] The data for these six animals are presented under the heading 40″-b. The remaining four animals in the 40-sec. group, with data presented under the heading 40″-a, showed no abnormal rate of spontaneous responding. Two of these dogs failed to achieve the criterion at all within 70 trials of training, thus accounting for the "plus" observed in the table. The data under the heading 40″ lumps all ten dogs. The 40″-a group seems to be the most nearly

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[2] The experimental data are presented in much greater detail in the author's dissertation (5).

[3] With appropriate statistical procedures, it can be shown (5) that the chance of "spurious acquisition" occurring is high for the 40-sec. group but exceedingly minute for all other CS-US groups.

TABLE 1

Number of Trials Required to Reach the Last Shock Trial as a Function of CS-US Interval

TRIALS	CS-US INTERVAL					
	5″	10″	20″	40″-a	40″-b	40″
Mean	9.4	16.0	25.8	55.5+	10.0	28.2+
Median	6.0	8.5	28.5	57.5+	7.0	18.5

TABLE 2

Mean Data for Various Indices of Acquisition as a Function of CS-US Interval

INDICES	CS-US INTERVAL					
	5″	10″	20″	40″-a	40″-b	40″
Mean number of shocks	6.5	11.0	18.7	44.3+	7.7	22.3+
Mean shock duration	133″	264″	283″	131″+	122″	126″+
Mean number of alternations	5.0	7.8	10.6	16.5+	6.7	8.6+
Mean trial of 1st avoidance	4.5	5.1	6.9	17.0	4.3	9.4
Mean trial of 5th avoidance	10.8	13.5	15.4	28.8	12.5	19.0

comparable to the other CS-US interval groups.

Table 1 indicates clearly that the number of trials required to reach criterion increases with CS-US interval. These data were subjected to Whitney's bivariate extension of the *U* test (16). The data for the 5-, 10-, and 20-sec. groups only were tested. The results indicate that unless a chance of 1 in 5,000 has occurred, a significant trend exists. We may note that, in so far as spontaneous jumps were involved in passing the acquisition criterion, precisely the reverse trend should have occurred. That is, the longer the CS-US interval, the more time there is for a spontaneous jump to effect a spurious avoidance.

Table 2 presents mean data for various subsidiary indices of acquisition. These data, of course, are not independent of the data for last shock trial, which have already been tested. The number of shocks received during acquisition, the total duration (in seconds) of shock received, the number of alternations between escapes and avoidances, and the trials on which the first and fifth avoidances occurred are given. (*Alternations* were scored whenever an avoidance immediately followed an escape trial, and vice versa.) The trends for all these indices are evident from inspection. They vary as a monotonic function of CS-US interval.

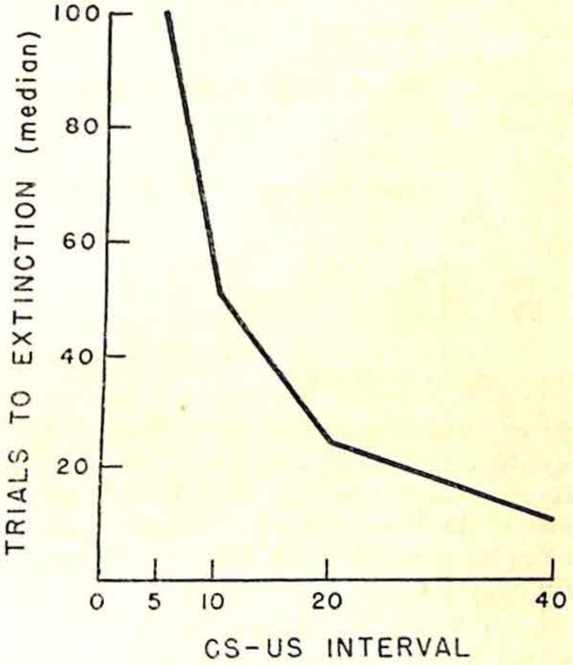

FIG. 1. Resistance to extinction as a function of CS-US interval

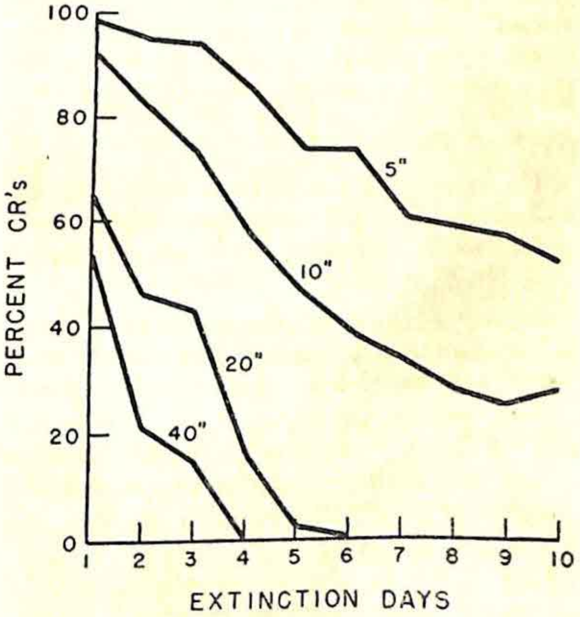

FIG. 2. Percentage of avoidance responses by extinction days as a function of CS-US interval

Extinction

The median number of trials required to achieve the extinction criterion is plotted as a function of CS-US interval in Figure 1. The trend is evident: the longer the CS-US interval,

TABLE 3

Median Latency of Avoidance during Acquisition as a Function of CS-US Interval

LATENCIES	CS-US INTERVAL					
	5"	10"	20"	40"-a	40"-b	40"
Median latency of 1st avoidance	2.50"	2.45"	8.30"	8.95"	10.35"	10.35"
Median latency of 5 criterial avoidances*	1.85"	2.70"	6.40"	12.65"	5.20"	6.65"

* p of apparent trend (Whitney's test, 5-, 10-, and 20-sec. groups only) is .0002.

the less resistance to extinction. The p of the apparent trend (Whitney's test, on the 5-, 10-, and 20-sec. groups) is less than .0002. Five of the 5-sec. and two of the 10-sec. dogs failed to extinguish within 100 trials. The same tendency is shown in Figure 2, which presents the percentage of responses made by each CS-US group on each extinction day. The percentage was determined by dividing the total number of avoidance responses by the total number of trials per day. (There were virtually no differences in the extinction data of the 40"-a and 40"-b groups. The data for these groups are pooled in Figures 1 and 2.)

Latency Data

The latency of *escape* from shock was *not* a function of CS-US interval. Within each group, similar curves of decreasing latencies were obtained for successive shocks. With all groups, an asymptotic escape latency of about 2.5 sec. (measured from shock onset) had been reached by the time six shocks were received.

The latency of *avoidance* is a separate matter. Table 3 presents the median latency of the *first* avoidance and of the *five criterial* avoidances by CS-US groups. These data are a function of CS-US interval: the longer the CS-US interval, the longer the latency of avoidance during acquisition.

The latency of response during *extinction* presents a similar picture. When the mean reciprocal of latency is plotted, by CS-US groups, for successive extinction days, there is not a single crossover among the four curves. The longer CS-US intervals exhibit longer latencies. This apparent trend, however, is partly dependent upon the inclusion of "infinite" latencies in computing the mean reciprocal of latency. Therefore, the data plotted in Figure 3 *exclude* infinite latencies. (The 40-sec. group is omitted because of the very small number of responses elicited from these animals.) The usual trend is evident during the first days of extinction. The early difference between the 5- and 10-sec. groups, however, has disappeared by the fifth day of extinction training. Both groups level off at latencies close to 2 sec. The duration of the CS, it should be noted, was 2 sec. Figure 3 shows a lengthening of latency throughout extinction for the 20-sec. group, but no such tendency exists for the 5- and 10-sec. groups.

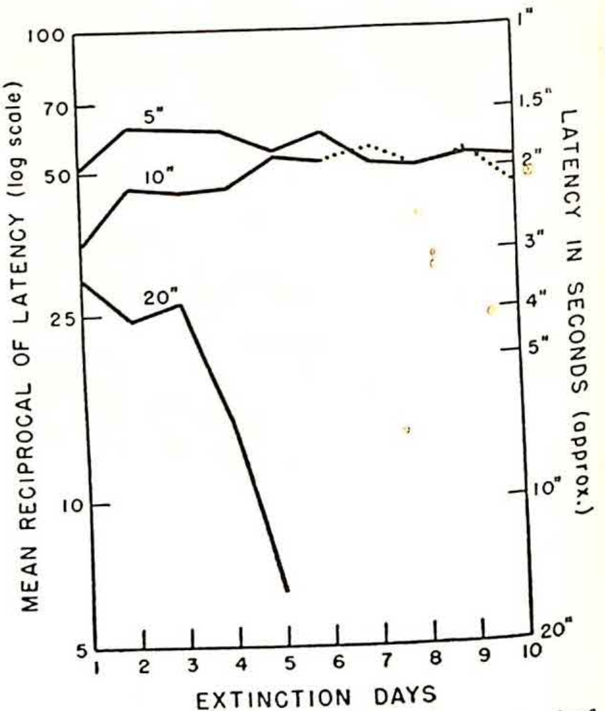

FIG. 3. Mean reciprocal of latency by extinction days as a function of CS-US interval (excluding infinite latencies). (Note that the ordinate for latency in seconds is approximate, since the antireciprocal of the mean reciprocal of latency is not necessarily the same as the mean latency in seconds.)

Spontaneous Jumping

There are several methodological difficulties involved in the analysis of spontaneous jumping. The length of time spent in acquisition varied systematically among experimental groups. Thus, to compare spontaneous responding during acquisition across groups, some measure of *rate* is needed. The rate measure, however, cannot be made wholly

TABLE 4

Median Maximum Spontaneous Jumping Rate during Acquisition as a Function of CS-US Interval

JUMPING RATE	CS-US INTERVAL					
	5"	10"	20"	40"	40"-a	40"-b
Median*	2.0	3.0	6.0	9.0	3.5	11.5

* p of apparent trend (Whitney's test, 5-, 10-, and 20-sec. groups only) is $< .05$.

TABLE 5

Median Spontaneous Jumping Rate by Extinction Days as a Function of CS-US Interval

EXTINCTION DAY	CS-US INTERVAL		
	5"	10"	20"
1	.13	.30	1.63
2	.87	1.81	
3	1.47	1.47	
4	.69	1.08	
5	.67		
6	.45		
7	.50		
8	.43		
9	.27		

independent of amount of experimental time. Table 4 presents one index of rate, the median *maximum rate* of spontaneous jumping during acquisition. The maximum rate was determined by computing the greatest number of jumps made by each animal during any single minute of acquisition. The tabled values thus express number of jumps per minute. The table indicates a significant tendency for spontaneous jumping rate to *increase* with CS-US interval.

The length of an *extinction* session was constant across CS-US groups. Table 5 presents the median *rate per minute* of spontaneous jumping for progressive extinction days. Because of the variability in the data, only medians which represent at least six animals are included. The very early extinction typically obtained with the longer CS-US intervals accounts for the lack of data from these groups. The table indicates, once again, a tendency for spontaneous jumping to be positively related to length of CS-US interval. The dog-to-dog variability, and the small and variable N, make it difficult to demonstrate this rigorously. Note also that spontaneous jumping tends to extinguish with the passing of days. But it is evident that there is a radical *increase* of spontaneous jumping on the second day that the dog is placed in the apparatus. The latter two findings were true of almost every animal, and across all CS-US groups. They are shown clearly in Figure 4, a plot of spontaneous jumping rate during extinction for a representative dog. The pattern during extinction was, very commonly, for spontaneous jumping first to increase, and then to decrease. The initial increase occurs, of course, several trials after the last shock has been received.

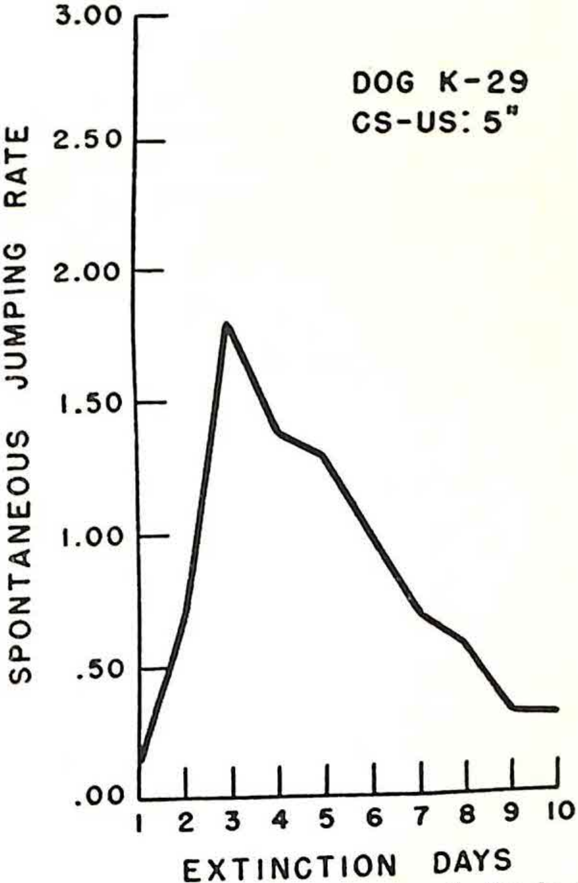

FIG. 4. Spontaneous jumping rate by extinction days for a representative dog

Emotional Behavior

There were characteristic differences between experimental groups in the kinds of emotional behavior exhibited in the apparatus. Typically, the 5-sec. animal sat tense, quiet, and motionless, facing the barrier, ears pricked forward. The animal jumped promptly and vigorously at presentation of the CS, perhaps with a single yip or gasp. The dog then resumed its tense posture in the opposite compartment.

The animal made few spontaneous jumps. The 20-sec. dog, on the other hand, displayed a great deal of agitation *between trials*. There was much agitated locomotion. The dog paced back and forth, bounced frantically up and down, climbed the walls, attacked the apparatus. There was often continual barking or whining. The diffuse agitation increased perceptibly at presentation of the CS, but the dog often vacillated at the barrier before jumping. These animals made a great many spontaneous jumps. The 20-sec. animals exhibited unmistakably pronounced gastrointestinal upset, which was almost completely absent in other groups. These dogs commonly belched and emitted continual stomach rumblings. Three of these animals actually vomited in the apparatus; another retched unproductively throughout an extinction session.

The pattern for the 10-sec. dogs seemed to lie midway between the two patterns just described. With the 40-sec. animals, the very high rate of spontaneous jumping and concomitant diffuse emotionality obscured all other aspects of behavior. The most general statement that can be made about these data is this: as CS-US interval increased, the quality of the emotional behavior passed from a *focalized* (about the CS) to a *diffuse* nature.

With all animals, there was a notable correlation between emotional symptoms and spontaneous jumping. When a dog, e.g., defecated or urinated, the spontaneous jumping rate tended to increase sharply at the same time. Emotional reactions to the CS, in all groups, first appeared a few trials before the animal began to avoid. The trial of the first detectable emotional reaction to the CS occurred earlier for the shorter CS-US groups. With the longer CS-US groups, several dogs exhibited pronounced emotional reactions to the CS (barking, trembling, lifting paw from grid) for long blocks of trials before making a single avoidance. Within all groups, defecation, urination, pilo-erection, trembling, panting, and drooling were common. There were no obvious differences between groups for these latter measures.

Control Group Data

The control groups provide information as to the probability of jumping occurring solely as a result of the dog's having been shocked in the experimental situation, without the pairing of CS and US. The control dogs did make some spontaneous jumps during "acquisition." They made, however, far fewer jumps than were made by experimental dogs which received an equivalent number of shocks. The median maximum rate of the control dogs during "acquisition" (cf. Table 4) was only 1.0. The controls made almost no spontaneous jumps during "extinction." Their median rate on each "extinction" day (cf. Table 5) was *zero*. There were no significant differences between the two control groups.

We may note, too, that on only 6 scattered occasions out of 1,000 trials did a control animal jump within 30 sec. of the buzzer onset. Thus, for the experimental animals, both avoidance responses and spontaneous jumps must have depended upon the *paired* presentation of CS and US—not on the characteristics of the US and the "situation as a whole."

DISCUSSION

Theory of Avoidance Learning

The experimental data are in accord with the kind of two-process theory suggested by Mowrer (8) and elaborated by Solomon and Wynne (14). We would expect, by conditioning principles, the strength of conditioning of the *emotional reaction* to the CS to diminish as CS-US interval is lengthened. The trial, and the latency, of the first *avoidance response* may be taken to indicate just such a trend, if we are willing to infer conditioned anxiety from the fact of avoidance. When the first avoidance occurs, the dog has already learned (by shock-termination) to jump to a cue pattern of shock-plus-fear. We can infer that, when the CS elicits intense fear, the animal will generalize the jumping response to the cue of fear-without-shock; the first avoidance then occurs (14, p. 16).

Were this the whole story, extinction of the avoidance response would begin immediately after the last shock, since the avoidance response dissociates the CS and US. When, however, the avoidance response is *followed by CS-termination*, the avoidance response is reinforced by anxiety-reduction. This reinforcement will occur *only if* the jump terminates the anxiety-eliciting CS (cf. 9, p. 7).

These theoretical considerations force us to note that, after the *first* avoidance, the effects of CS-US interval on the emotional response become confounded with differential reinforcement of *avoidance* among the various CS-US groups. This is so because the trace-conditioning procedure is such that, for some dogs, the avoidance response occurs *after* the CS has ceased to act, and thus cannot in theory be reinforced.

The fact is (Table 3) that only in the 5- and 10-sec. groups did any number of dogs begin to avoid with latencies briefer than the CS-duration; and only in these groups do we find marked resistance to extinction (Fig. 1). The latency data depicted in Figure 3 complete the picture. With the 5- and 10-sec. dogs, no extinction is evident; with the 20-sec. dogs, whose early avoidance latencies exceeded the duration of the CS, an extinction process is evident throughout the latency curve. (The latency of the first avoidance is presumably determined by the latency of the emotional reaction, itself a function of CS-US interval.)

This somewhat labored formulation is supported by the data of a study of the CS-US interval in avoidance employing a *delayed-conditioning* procedure (2, 13). The delayed-conditioning procedure is so structured that, no matter *when* the dog responds to the CS, the response is at once followed by CS-termination (anxiety-reduction). This inevitable reinforcement would be expected to make all animals highly resistant to extinction, and thus to obscure differences between CS-US groups. We would thus expect Brush, Brush, and Solomon's finding that, with CS-US intervals from 2.5 to 80.0 sec., "failure of extinction" within 200 trials was the rule for all CS-US groups. The "failure of extinction" seems to depend upon the use of a delayed-conditioning procedure, which allows the avoidance response to terminate the CS.

The data on alternations (Table 2) indicate that, at least in the present and similar studies (2, 13, 14), aperiodicity of primary reinforcement (12) is not the most important determiner of resistance to extinction.

Spontaneous Responding and Anxiety

There have been very few studies of spontaneous, intertrial responding. The phenomenon, noted briefly in experimental papers, seemed readily assimilable to existent theories. The usual assumption has been that spontaneous responses result from conditioning to generalized apparatus cues (cf. 4, p. 76; 11, p. 89). That is, apparatus and/or proprioceptive cues which have occurred in contiguity with shock (or shock-termination) might be expected to elicit the response. This *ad hoc* assumption, however, seems inadequate in the light of the data. Why do the control dogs, for which apparatus cues and shock occur in contiguity, fail to make spontaneous responses? Why is there an effect of CS-US interval on spontaneous responding?

The data seem to support Mowrer and Lamoreaux's (10) assumption that spontaneous responses may serve as an index of underlying anxiety. The correlation between symptoms of emotionality and spontaneous jumping has already been cited. The high rates of spontaneous jumping, further, were associated with a particular *quality* of emotionality—the "diffuse" pattern. The dogs trained with long CS-US interval seemed continually agitated and responded continually. The spontaneous responses seemed, in Mowrer and Lamoreaux's sense, to reflect a *nondiscriminated* anxiety.

The differences in emotional patterns between short and long CS-US groups are reminiscent of the clinical distinction between "bound" and "free-floating" anxiety (3). The control group data are particularly suggestive in this respect. The control groups showed very little diffuse emotional upset in the apparatus, and very little spontaneous responding. That is, they did *not* exhibit the "free-floating" pattern of emotionality. The data thus suggest that free-floating anxiety may result only when a signal and trauma occur in such a way that it is *difficult, but not impossible*, for the organism to "bridge" the two events. Trauma alone is not sufficient to elicit the diffuse pattern of emotional agitation, nor is trauma preceded by a distinct, highly contiguous signal.

These observations, irritating though they may be to current S-R formulations, are not without parallel. Working with goats, Liddell (6) has reported that regularly repeated shocks without a preceding signal leave the animal undisturbed. The same shocks, when preceded by a CS, lead to "experimental neurosis." The nature of anxiety and avoidant emotion-

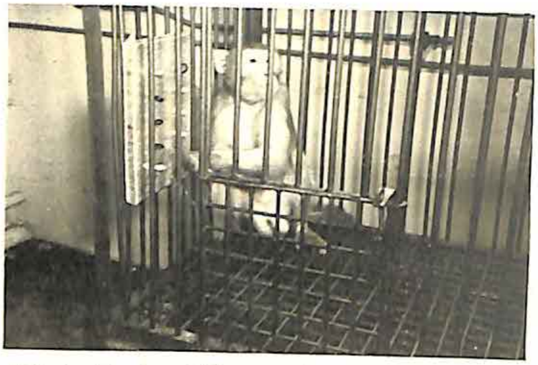

FIG. 1. Monkey 153 responding to screw eye on test board

a test block. The four training periods for each discrimination problem were conducted on Thursday, Friday, Monday, and Tuesday, respectively, between 11:00 and 12:00 A.M.

An individual trial was begun by removing the screen to present the test board and terminated by replacing the screen 1 min. after the first response of the animal to a screw eye, a "response" being defined as touching the object with fingers or mouth. A trial was terminated 5 min. after initial exposure if the animal failed to respond. The *E* used the Audograph to record, in coded form, touches, removals, and other relevant behavior such as evidences of distraction and lack of motivation, and subsequently transcribed and tabulated the records. A trial was concluded by interposing a screen between the monkey and the test board. A standard daily session consisted of one trial on each of four test boards presented in random order. The only exception to this practice was on days 1 and 2 of problem 1. On these days, eight test boards were presented. This procedure was subsequently abandoned because of observed diurnal satiation effects.

The colors of the paired members of the screw-eye stimuli and the experimental sequence are as follows: (*a*) red-green, (*b*) brown-yellow, (*c*) pink-blue, (*d*) black-orange, (*e*) white-orchid, (*f*) maple-cream, and (*g*) light green dark blue, the first color of each pair being positive for monkeys 102 and 147, the second positive for monkey 153. A two-week rest period was interposed between problems 5 and 6.

RESULTS

Figure 2 presents the mean percentage of correct responses made on days 1 to 4 of problems 1 to 5 and problems 6 and 7. The scores were obtained by dividing the total number of correct responses made by all animals on a given day by the corresponding total number of responses made prior to and including the final correct response. A correct response was defined as the *removal* of a correct object. An incorrect response was defined as the touching of an incorrect (nonremovable) object or the touching of a correct object without removal. By this scoring system the number of correct responses is finite and the number of incorrect responses is limited only by time.

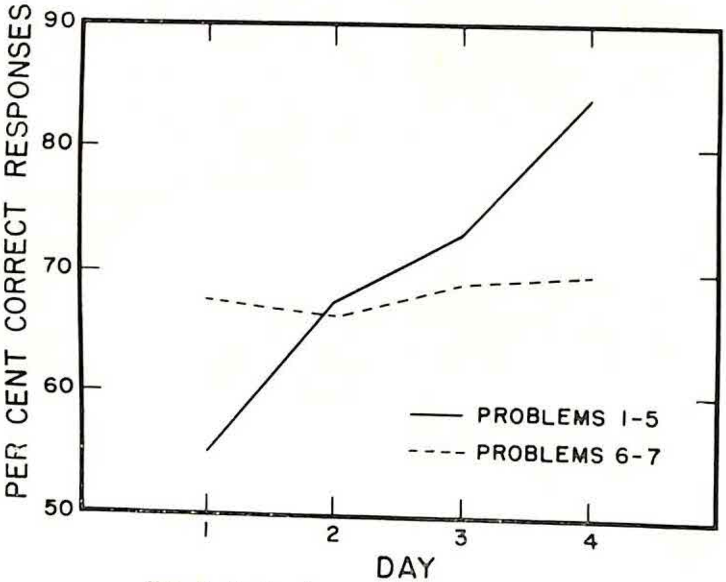

FIG. 2. Ratio of correct to total responses

The curve for problems 1 to 5 shows a progressive increase in the percentage of correct responses. The difference between the day 1 and day 4 scores was found by a *t* test on arcsin-transformed percentage correct response scores to be significant at the .05 confidence level. The same data were also scored by a second system, in which the only responses

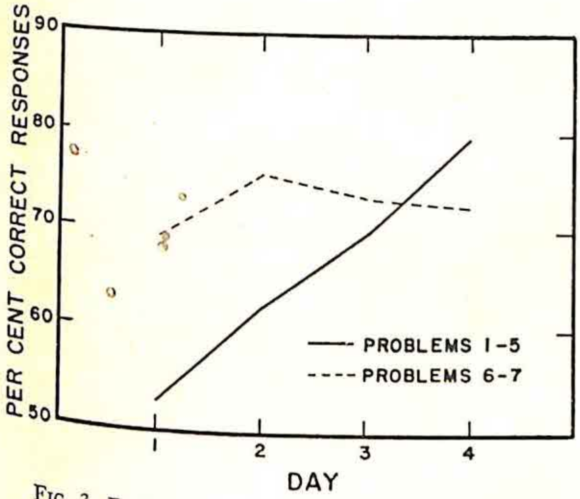

FIG. 3. Percentage of correct initial responses to pairs of stimuli

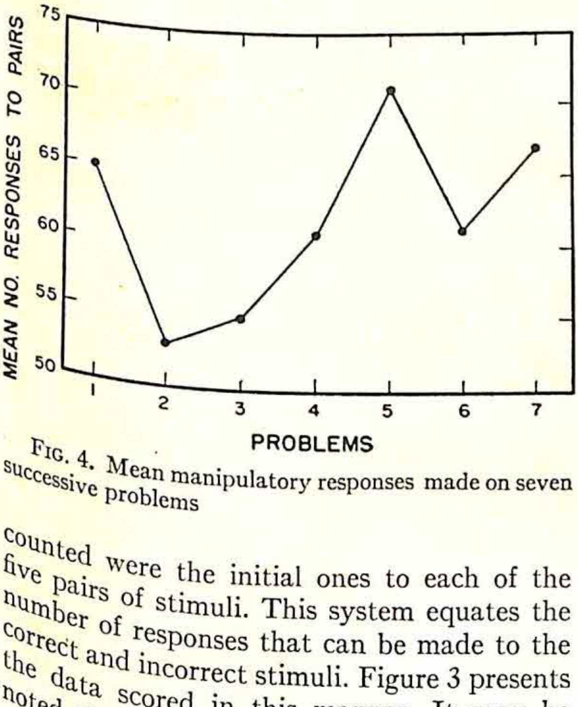

FIG. 4. Mean manipulatory responses made on seven successive problems

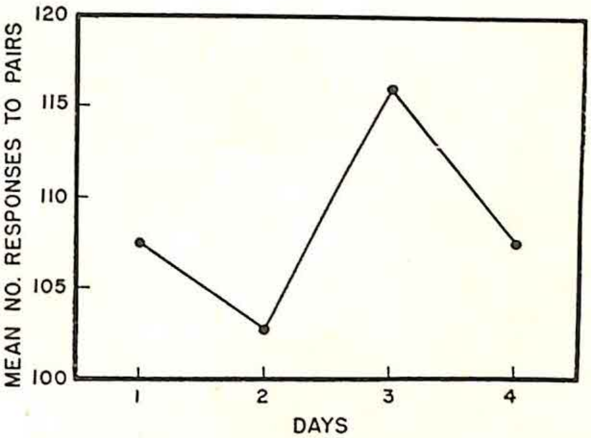

FIG. 5. Mean number of pairs of stimuli manipulated

counted were the initial ones to each of the five pairs of stimuli. This system equates the number of responses that can be made to the correct and incorrect stimuli. Figure 3 presents the data scored in this manner. It may be noted that the curves derived from the two methods of scoring are very similar.

The curves for problems 6 and 7, Figures 2 and 3, give the percentage of correct responses on the two problems following the two-week rest interval. The difference between day 1 of problems 1 to 6 and day 1 of problems 6 and 7, and the difference between day 4 of problems 1 to 5 and day 4 of problems 6 and 7 were not significant at the .05 level as determined by a t test on arcsin-transformed scores (Fig. 2). Failure to obtain significant differences between scores for the first days on the two sets of problems is interpreted as lack of evidence for learning set formation.

Figure 4 shows the total number of pairs of stimuli responded to in each problem. Persistence of the manipulation motivation is indicated by the fact that t tests reveal no significant drop in the curve, not even following the two-week rest period interpolated between problems 5 and 6. Figure 5 presents, by days, the mean number of pairs of stimuli responded to by the three animals for the seven problems. There are no significant differences between adjacent points on the curve, as determined by t tests.

DISCUSSION

The present study has demonstrated progressive improvement in performance on seven nonspatial, object-quality discrimination problems in the absence of homeostatic drive reduction. These findings are, in general, consistent with those of the early manipulation drive study (4), which showed a high level of performance efficiency on a puzzle problem after 12 days of training, and a later study (2), which yielded a typical negatively accelerated learning curve for the entire course of acquisition on a more complex puzzle problem. The fact that the form of the learning curves of the present study is more nearly linear than negatively accelerated may be a function of the short duration of each problem.

Harlow (2) showed that repeated massed presentations of a puzzle during a single day resulted in a significant decrease in the number of puzzle devices manipulated. In consideration of these results, the present experiment was designed so as to minimize any such satiation effect. Restriction of the number of presentations to four boards a day and a two-day rest interval between days 2 and 3 of each problem were provided for this purpose. In addition, the two-week rest period was interpolated between problems 5 and 6 to permit "recovery" from any satiation effects accruing through problem 5. Actually, there was no apparent satiation throughout the entire series of seven problems. On the contrary, there was a marked persistence of manipulation motivation, and the two-week rest period evidently had little effect.

The theoretical implications of this and related studies have been discussed in a recent symposium (3).

SUMMARY

1. Three rhesus monkeys showed significant, progressive improvement in seven discrimination problems on the basis of manipulation motives.

2. Significant improvement on successive problems was not demonstrated.

3. Manipulation motivation as measured by response frequency persisted with no significant decrement throughout the seven problems of the study.

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Received November 15, 1952.

THE EFFECTS OF EARLY RESTRICTION ON ACTIVITY IN DOGS[1]

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In the last decade it has been well established experimentally that restriction of early experience has a detrimental effect on the later learning ability of rats, whereas enrichment of early experience has a favorable effect.

Recently, a program has been initiated at McGill with the purpose of investigating more thoroughly the effects of restriction in early life on the various psychological characteristics of dogs. This genus offers a much broader repertory of behavior than the rat and is consequently a more fruitful subject for study of the problem under consideration. A preliminary report (2) suggested that early restriction affects not only learning ability, but also motivation, emotionality, and social behavior. One observation reported in this study we regard to be of particular importance in that it concerns an effect that may be basic to all other psychological changes. This was the finding that "restricted" dogs explored more (were more active) than normal animals in a familiar situation, and that in an unfamiliar one, their level of activity, while being initally about equal to that of normals, fell off at a much slower rate with repeated exposure to that situation. The authors interpreted these results as representing a difference between the two groups in "stimulation value" or "capacity for boredom." Since these data were based on small samples and, in addition, showed nothing about the persistence of the effects observed, it is important that they be verified and extended.

ANIMALS

Twenty Scottish terriers, 13 males and 7 females, all offspring of one original litter of the Bar Harbor strain, were used in the experiments reported here. The rearing procedure was as follows: at the time of weaning (four weeks) each litter was divided randomly into an experimental and a normal control group. Up to eight months of age, the control animals were raised as pets either in homes or in the laboratory. In this way, their early experience was made as wide and as diversified as possible. Two of the normal dogs (in the young group), however, had to be returned to the laboratory after living in homes for only four months. Consequently, they cannot be regarded as being as "free" as the others, although during the last four months prior to testing they were given as much freedom as possible and allowed to exercise outside daily with older animals.

Three degrees of restriction, severe, moderate, and slight, were imposed on the 12 experimental dogs up to seven to ten months of age.

Severe restriction consisted in raising two animals, each in complete isolation, in small wooden boxes approximately 26 by 26 by 40 in. which were lighted on alternate days only. To ensure that these dogs gained no additional perceptual experience during daily cleaning and feeding, each box had an adjoining compartment identical in size and shape which the dogs would enter each day for their daily ration of food. The sliding door between the two sides was then closed and the side previously occupied by the animal was cleaned in preparation for the next day. A small panel in the top of each compartment permitted observation during the period of restriction.

The seven moderately restricted dogs were raised in groups of two or three in ordinary metal living cages 24 by 32 by 72 in. The front of each cage was covered with cardboard to prevent the occupants from seeing out, but the top was left uncovered in order to allow light to enter. Thus, these animals differed from the severely restricted *S*s in that they had more space available and had cagemates.

The three slightly restricted animals were also reared in living cages, but neither the fronts nor the tops of the cages were covered. Further, unlike the other restricted dogs, these animals were handled occasionally and taken out periodically into an adjoining room for clipping and medication. They were not allowed access to any other environment, however, so that their experience was limited in comparison with that of the normal animals.

Early restriction as described above appeared to have no appreciable effect on the health or vigor of the experimental animals. Their weights and appetites were normal. Their initial behavior on being removed from restriction has already been reported (2). At the end of eight to ten months all dogs, normal and experimental, were kept in the laboratory and given identical treatment.

All *S*s could be further divided according to their age at the time of testing into three groups, as shown in Table 1. It should be noted that severe and slight restriction were imposed only on the young group of *S*s.

Previous to the experiments described below, all animals had taken part in other tests and had had contact with other dogs and with the *E*s. No *S* showed any timidity in the tests described below.

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[1] This research was supported by a grant-in-aid from the Rockefeller Foundation. A summary of it was presented at the EPA meetings in Boston, Mass., in April, 1953.

TABLE 1

Breakdown of *S*s according to Age, Sex, and Rearing Conditions

AGE GROUP	REARING CONDITIONS	MALE	FEMALE
Old (2–4 years)	Normal	1	1
	Moderate restriction	2	
Middle (1½–2 years)	Normal	2	2
	Moderate restriction	2	3
Young (9–10 months)	Normal	1	1
	Slight restriction	3	
	Severe restriction	2	

EXPERIMENT 1

Procedure

Eighteen dogs were used in this experiment, 7 normal and 11 restricted, 1 old normal and 1 old restricted having been omitted. The study was carried out in a small room (approximately 8 by 6 ft.) familiar to all the *S*s inasmuch as all of them had been in it on numerous occasions for trimming, clipping, and medication. The floor was cleared of all movable objects. Each animal was taken to the room and allowed to move about and explore freely during four daily ½-hr. sessions. The observer sat quietly on a stool at one side of the room. The time was recorded during which a dog was active, i.e., not sitting or lying down.

Results

The mean times in seconds spent by normal and restricted dogs in activity are presented in Table 2. It is clear that the restricted dogs were much more active in the situation than the normal animals.

The animals used came from four litters. A comparison of normal and restricted within a litter showed that there were no cases of overlap in activity scores in Session I, 1 case in each of two litters in Session II, and 1 case in one litter and 2 in another in Sessions III and IV. With total scores, there was 1 case of overlap in each of two litters. To examine the differences statistically, both in this experiment and in the next, the authors used analysis of variance, with method of rearing (two groups) and age (three groups) as variables. This allowed the effect of each to be dealt with independently of the other. In the young group, the mildly and severely restricted dogs were combined. Dogs of different litters were also combined where necessary. To correct for the unequal numbers in the groups, Tsao's method of expected proportional frequencies (5) was used. The differences between mean scores of each session separately and over all four sessions together were examined in this way. It was found that restricted dogs were more active than normals in Sessions I ($F = 75.34$, $p < .001$) and III ($F = 6.30$, $p < .05$) and over all four together ($F = 12.66$, $p < .01$). In Session II, the difference was significant when the two dogs of the older group were omitted ($F = 5.43$, $p < .05$). Similarly, younger dogs were significantly more active than older in Sessions I ($F = 59.17$, $p < .001$), II ($F = 8.88$, $p < .01$), III ($F = 7.55$, $p < .01$), and IV ($F = 19.19$, $p < .001$), and over all four sessions together ($F = 22.89$, $p < .001$). A triserial correlation computed between age and activity gave a coefficient of $-.589$, ($p < .01$).

In this analysis, only the interaction in Session I was significant ($F = 10.78$, $p < .01$), indicating that the effects of restriction on activity showed up most clearly in the middle-aged group. In this session, the interaction was combined with the "within" to test the main effects. In the other sessions and over all four together, however, the interactions were not significant, indicating that the main variables were independent and that the effects of restriction are fairly permanent. Thus, cage-reared animals in the middle-aged group (removed from restriction for over one year) were more active than their normally reared littermates over all four sessions combined ($t = 3.85$, $p < .01$). This did not apply in the case of the old group, however.

There was a tendency for severely restricted dogs to be more active than slightly restricted, but this difference was not great. Since all the moderately restricted animals were in the two older age groups, it was not possible in either experiment to compare their scores legitimately with those of the slightly and severely restricted dogs, which were all in the younger group.

All the dogs grew less active from one session to the next. The activity of the restricted animals, however, declined at a faster rate than did that of the normals, so that the difference between groups was greatest on the first day and smallest on the last day of testing.

To compare the rate of decline of activity of normal and restricted animals within a session, each ½ hr. was divided into three 10-min. periods and the activity during each period was measured. An average was taken of the four sessions. Data were obtained for nine dogs. Three were normal (one old, two young), and six were restricted animals (one old, five young). In general, the activity of the restricted dogs tended to decline at a slower rate from the first to the last 10-min. period than that of the normals, but the difference between the groups was not statistically significant.

In order to check the reliability of the test, rank-order correlations were computed between each session and every other, for all 18 dogs. The following results were obtained: $\rho_{\mathrm{I\,II}}$, .819; $\rho_{\mathrm{I\,III}}$, .705; $\rho_{\mathrm{I\,IV}}$, .552; $\rho_{\mathrm{II\,III}}$, .771; $\rho_{\mathrm{II\,IV}}$, .512; $\rho_{\mathrm{III\,IV}}$, .711. All these are significant ($p < .05$).

To summarize, significant differences in activity ("capacity for boredom") between normal and restricted dogs were demonstrated in three out of four daily ½-hr. sessions in a limited and relatively homogeneous environment. Age was related inversely to amount of activity.

EXPERIMENT 2

Method

Apparatus. In this experiment, a seven-unit maze was used. As shown in Figure 1, it consisted of eight barriers arranged so as to form two rectangles, with the path on the perimeter and across the center. In Session I, which was in a large room, wooden barriers were used. The dimensions of the outside, formed by the walls of the room, were 20 by 18 ft. and the dimensions of the inner rectangles, formed by the barriers, were 15 by 4 ft. Testing in this session was carried on at night with blinds drawn over the windows of the room and constant overhead lighting. Session II took place outside in a small field between the road and the laboratory. Testing in this session was done during the daytime. It is probable that the situation here was considerably more complex than that involved in Session I. Although the basic maze pattern used was the same, there was a great variety of visual and auditory stimuli (traffic, etc.) available. The perimeter of the maze in Session II measured 17 by 17 ft. and the inner barriers 11¾ by 5 ft. In this cage, both the outer and the inner parts were made of chicken-wire.

Procedure. All 20 dogs were used in this experiment. In each session, they were given two 10-min. trials, one a day on two consecutive days. The procedure in each trial was as follows: a dog was introduced into the maze at the starting point marked S in the diagram. It was then allowed to move about freely for 10 min., after which it was taken out and returned to its cage. During each trial, the observer sat quietly outside the maze at O. A record was taken of the path of each animal during each of the six 100-sec. periods which together comprised a single 10-min. trial. Scoring was in terms of feet traversed. All animals were fed 4 to 6 hr. previous to testing.

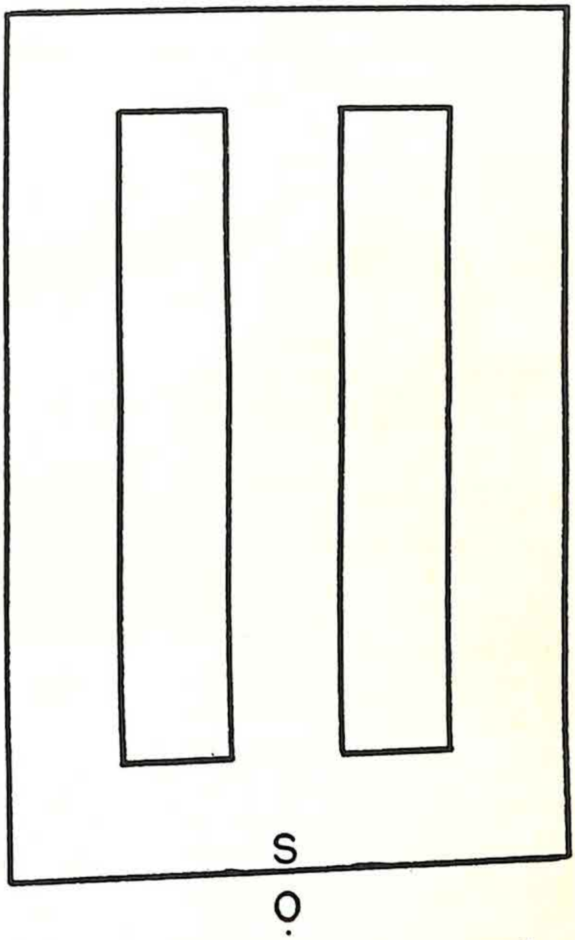

FIG. 1. The maze pattern used in Experiment 2

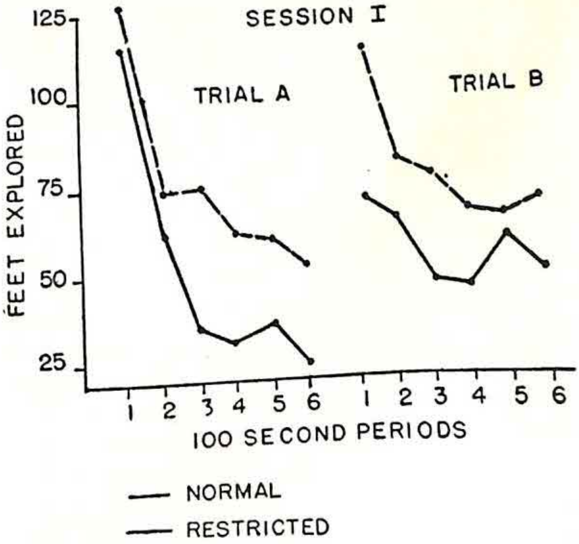

FIG. 2. Activity curves of normal and restricted dogs in the two trials of Session I

Results

Session I. Curves of activity in the two trials of the indoor session are presented in Figure 2.

TABLE 2

Mean Times in Seconds Spent by Normal and Restricted Dogs in Activity during Four Half-hour Trials in a Uniform Situation

CONDITION	SESSIONS				
	I	II	III	IV	M
Normal	884.14	993.28	752.71	755.86	846.50
Restricted	1519.18	1360.91	1218.27	1015.45	1278.45

TABLE 3

Mean Total Feet Explored by Three Age Groups of Normal and Restricted Dogs in Two Sessions of Two Trials Each

AGE GROUP AND COND.	SESSION I		SESSION II	
	A	B	A	B
Older				
N	150.5	162.5	483.5	302.0
R	140.5	390.5	799.5	472.5
Middle				
N	250.0	275.0	427.3	307.8
R	433.2	461.4	762.2	468.2
Young				
N	500.0	599.5	757.5	524.5
R	583.0	499.6	518.8	465.6

Mean scores of normal and restricted animals in the three age-groups for each trial of the two sessions are shown in Table 3. It is clear from these that restricted dogs were much more active than normal animals. In trial A the two groups started out at about the same level for the first two 100-sec. periods, after which point the activity of the normals declined at a much faster rate than that of the restricted dogs. A comparison of normal and restricted dogs within each of the five litters used in this experiment showed only one case of overlap in one litter. Since the groups were not as markedly different during the first two periods, only the last four were compared statistically. The F tests were used in much the same manner as in Experiment I (Tsao's method of expected equal frequencies), with method of rearing and age as variables. Restricted dogs were significantly more active than normals in this trial ($F = 18.59$, $p < .001$), a difference which held when the three mildly restricted animals were omitted from the analysis to equalize the groups ($F = 5.80$, $p < .05$), and younger were significantly more active than older dogs ($F = 11.61$, $p < .01$). A triserial correlation computed between age and activity gave a coefficient of $-.759$ ($p < .01$).

Since the interaction in the above analysis was not significant, we may conclude that age and method of rearing were independent. The effects of restriction do not disappear with age. In fact, the difference between the normal and restricted dogs is more marked in the middle-aged and old group than in the young group, as shown in Table 3. The reversal in the old group in trial A was caused by the very low score of one restricted animal, but otherwise the trend is clear.

In trial B of this session, the difference between the two group was smaller ($F = 2.47$, $p < .10$) over all six periods. Omitting the younger dogs, the six middle-aged and old normals were significantly less active than the seven middle-aged and old restricted ($F = 6.68$, $p < .05$), and within the three litters from which these dogs came, there was only one case of overlap in one litter. As in the first trial, activity varied inversely with age ($F = 6.07$, $p < .05$). The triserial correlation between age and activity was $-.627$ ($p < .01$). As in trial A, the difference between normal and restricted dogs in the two older groups was still as large as, or larger than, that between normal and restricted animals in the young group.

Both groups were more active in trial B than in trial A and, as shown in Figure 2, their activity curves declined less steeply. In trial A the mean drop in amount of activity from period 1 to 6 was 79 per cent for normals and 60 per cent for restricted dogs (mean drop for both groups together was 67 per cent). In trial B, mean drop in activity was 34 per cent for normals and 40 per cent for restricted dogs (mean drop for both groups together was 38 per cent). Correlation between total scores between the two trials of Session I for all 18 dogs was .796 ($p < .01$).

In both trials, the two severely restricted dogs were more active than the three slightly restricted animals. Their mean total scores in trial A were, respectively, 688 and 513 ft., and in trial B, 635 and 409 ft. Although the two groups are small, there was no overlap between their scores in either trial. Consequently, it seems likely that there is a real difference

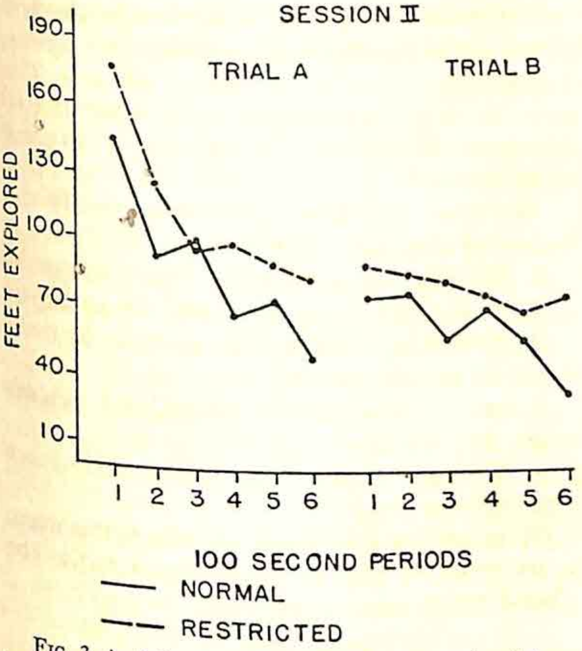

FIG. 3. Activity curves of normal and restricted dogs in the two trials of Session II

between them, and that this is a direct result of degree of restriction.

Session II. Curves of activity of the normal and restricted dogs in each trial of the outdoor session are presented in Figure 3. Restricted animals were still more active than normals in this session, but the difference between them is not significant. However, within the three litters of middle-aged and older dogs, there was only case of overlap in one litter in trial A and two cases of overlap in the same litter in trial B. All animals showed a higher activity level than in the indoor session ($t = 2.71$, $p < .01$). Correlation between trials was .627 ($p < .01$).

The rate of decline in this session was about the same, on the average, as in Session I. In trial A, the mean drop in activity from period 1 to 6 was 66 per cent for normals, 54 per cent for restricted (mean for both groups was 60 per cent), and in trial B, 60 per cent for normals and 14 per cent for restricted dogs (mean drop for both groups was 35 per cent).

Degree of restriction had no significant effects in this session, and amount of activity did not vary with age. It should be noted from Table 3, however, that in both trials of this session the animals of the young group, unlike the old and middle-aged, showed a reversal of the previous trend. The young restricted were somewhat less active than the young normals.

To summarize, significant differences in activity between normal and restricted dogs were found in both trials of Session I, which involved a fairly uniform environment, but in neither trial of Session II, which was outdoors and less uniform. In Session I, severely restricted dogs were more active than slightly restricted, and younger more active than older. Neither comparison was significant in Session II. .

DISCUSSION

The results presented verify the findings reported by Clarke *et al.* (2). Dogs restricted in early life are more active than normal animals, severely restricted more than slightly restricted, and younger more than older when the situation is simple and homogeneous as in Experiment 1 and Session I of Experiment 2; these differences did not appear in Session II of Experiment 2. The results further justify the conclusion that the effects of restriction endure for some time after the actual restricting conditions have been removed.

A question of some importance concerns the nature of the parameter studied in the experiments presented above. Although the term "activity" has been used in describing the behavior of the dogs, it might more accurately be called "exploratory behavior." This is implied by the fact that it characteristically showed a decline with time in all the tests given. There would be no reason to expect such a tendency were the behavior being studied merely general activity, since the latter, as measured by an activity wheel, is cyclical or random and largely independent of the environment. While it is possible that the decline was due merely to motor fatigue, we feel this is unlikely. A normal, healthy dog does not generally become tired in only 10 min. Furthermore, it is difficult to see why dogs raised as pets should become fatigued more quickly than animals raised in restriction. Consequently, though both general activity and exploratory behavior may have been involved in the experiments, the second almost certainly predominated. No mentalistic interpretation of exploration is implied. It is merely activity initiated by a state in the organism which we may call, after Berlyne (1), "curiosity," which is, in turn, aroused by novel environmental stimulation. As the latter impinges on an organism over a period of time, curiosity, and hence exploration, diminishes.

The question of how restriction operates to produce the lasting effects described is a difficult one to answer at present. As Hebb has already suggested in another connection (3), it seems likely that the early part of an individual's life is of great importance in determining his psychological make-up, and in fact, is more important than later life. Not only the relative effects of brain damage on young and older patients as described by Hebb (3), but also the relative effects of early and late restriction in rats as studied by Hymovitch (4) and Wolf (6) indicate that this is so. More drastic changes can occur when the individual is still immature. Since exploratory activity is directly dependent upon perception, it is not surprising that it should be markedly affected by restriction of early perceptual experience. The restricted dogs had perceived less of the environment and consequently had had less opportunity than the normal animals to form general perceptual schemata into which novel stimuli might be fitted. In this way, at least, they were psychologically retarded and, as the results showed, acted more like the young normal animals. Both their general behavior and performance on problem-solving tests support this hypothesis, although further research will be needed before it is definitely established.

SUMMARY

The experiment was designed to examine the effects of restricting the early experience of dogs on their (exploratory) activity later in life.

Restriction, of three degrees of severity, was imposed on 12 Scottish terriers for the first seven to ten months of life. Their 8 littermates, reared as pets, served as normal controls. The animals were tested at various ages in two experiments involving situations of varying complexity.

The results of these experiments justify the following conclusions:

1. Exploratory activity in dogs declines as a function of time of exposure to the situation.

2. Restricted dogs explore significantly more than normal animals.

3. Severely restricted dogs tended to explore more than slightly restricted animals.

4. Younger dogs explore significantly more than older animals.

5. In testing conditions in which the mean activity of all dogs is raised significantly, the above differences do not hold.

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Received December 16, 1952.

APPROACH AND AVOIDANCE GRADIENTS AND CONFLICT BEHAVIOR IN A PREDOMINANTLY TEMPORAL SITUATION[1]

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The concept of conflict behavior is of major importance both in theories of behavior disorders and in many of the problems met in psychological clinics. A great deal of experimental and theoretical work has been done in an effort to make the concept more meaningful and useful. An apparent relationship is seen clinically between behavior disorders and severe conflict. Evidence from experimental studies wherein laboratory animals are subjected to conditions such as those calling for difficult discriminations support these clinical observations. The "experimental neuroses" produced in many such studies have been considered analogous to the disturbances in human behavior shown in the clinical situation. These laboratory studies have been summarized by Liddell (8).

The most extensive treatment of the concept of conflict behavior, however, is that of Miller (9). He has compiled the work of Lewin, Sears, Hovland, Hull, and others, and has included learning principles in a comprehensive theoretical and experimental analysis of conflict behavior in simple spatial situations.

Miller, in his consideration of conflict behavior, advances four fundamental assumptions, all of which have been supported by the studies of Brown (3). These assumptions as stated by Miller are:

> 1. The tendency to approach a goal is stronger the nearer the subject is to it. This will be called the *approach gradient*.
>
> 2. The tendency to go away from a place or object avoided is stronger the nearer the subject is to it. This will be called the *avoidance gradient*.
>
> 3. The strength of avoidance increases more rapidly with nearness than does that of approach. In other words, it may be said that the avoidance gradient is *steeper* than the approach gradient.
>
> 4. The strength of the tendencies to approach or avoid varies with the strength of the drive upon which they are based. Thus, an increased drive may be said to raise the *height* of the entire gradient (9, pp. 433–434).

The supporting studies by Brown included an additional assumption, i.e., that the greater the tendency to respond, the harder the organism will push or pull against a restraint.

PROBLEM

The first objective of the present experiment is to examine in a predominantly temporal situation the first three of Miller's four assumptions. The second objective is to study the *S*s' behavior in a conflict situation emphasizing temporal aspects in order to determine whether or not this behavior supports the deductions which can be drawn from the three fundamental assumptions.

Previous studies of these assumptions have involved simple spatial situations which tended to neglect temporal factors. More complicated life situations frequently include partly nonspatial sequences in which temporal factors play a more important role. This experiment is designed to test whether or not these hypotheses may be of value in analyzing situations in which temporal factors are emphasized.

METHOD

Subjects

Four male albino rats, without previous experimental histories, were the *S*s used in this experiment. They were approximately 75 days old at the beginning of the experiment.

Apparatus

The apparatus used (see Fig. 1) was that devised by Bijou (1, 2) in developing a conditioning methodology for studying conflict behavior in the white rat. The rat is restrained in the following fashion: Its head is placed in a stock which is locked with a thumb screw, and a closely fitting wire cage fits over its body, which remains in a natural sitting position. The stock and body cage rest on a slide which moves forward approximately 3 in. from the "between-trials" position to the "trial" position. A food tray can be automatically presented through a slot in a panel just in front of the stock so that it rests just in front of the animal's head

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[1] This study was done when the writer was at Indiana University. Appreciation is expressed to Dr. S. W. Bijou for his generous advice and assistance. A condensed account was presented at the Amer. Psychol. Ass., Washington, D. C., September, 1952.

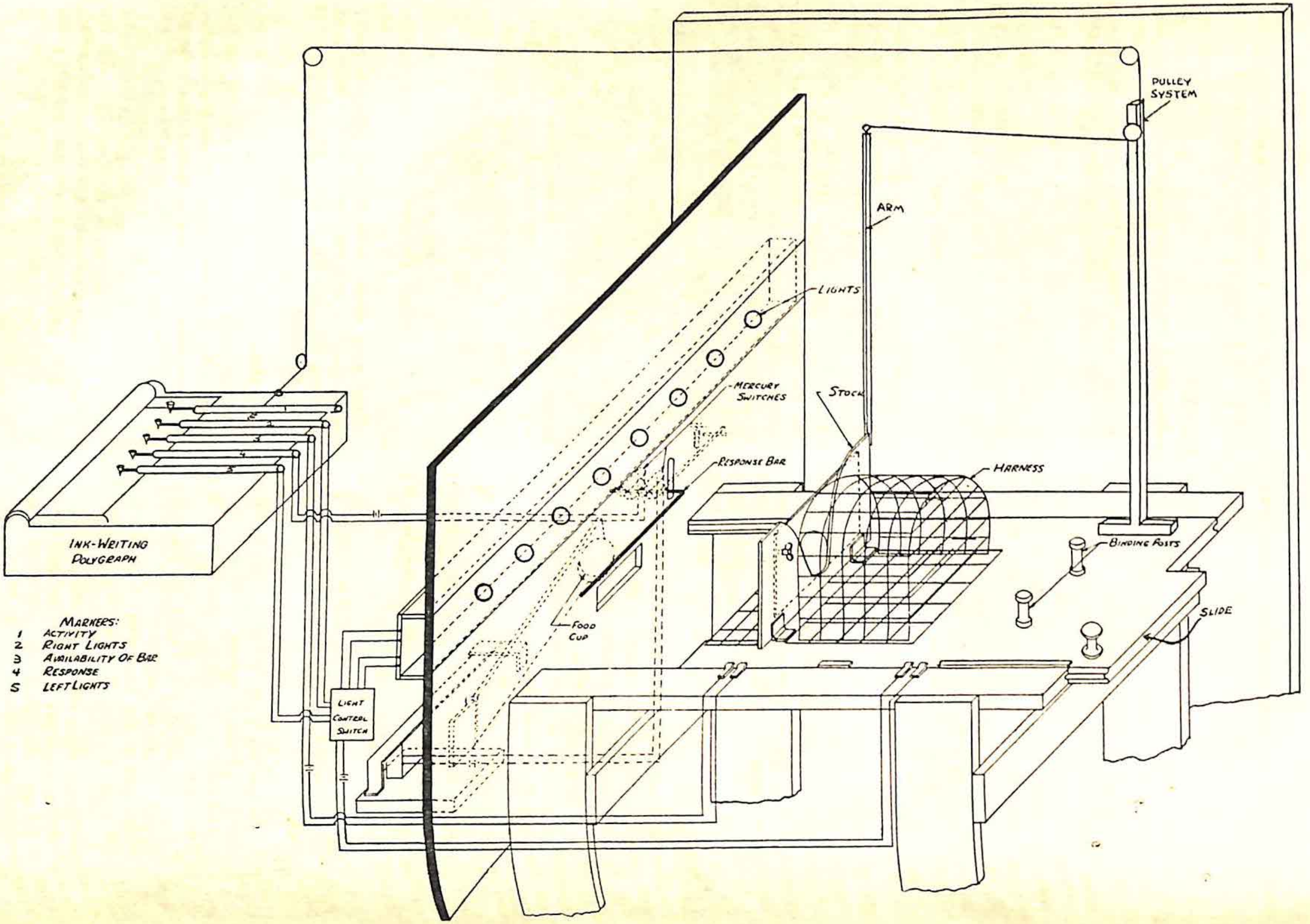

FIG. 1. The Bijou conditioning apparatus

when the slide is in its forward position. Punishment in the form of a continuous electric shock can be administered through a loop of wire fastened securely around the animal's body, just behind the front legs. A light in the center of the panel directly above the food tray serves as the positive stimulus associated with food, and a buzzer serves as the negative stimulus associated with shock.

Polygraph markers record the period during which the conditioned stimuli are activated, the onset of the punishment or the availability of the food tray, and the activity of the animal, i.e., forward and backward movement of the stock. The stock is hinged at the base and moves through an arc of approximately 20°. Thus, the direction, magnitude, and latency of the response can be accurately measured. The unit of measurement in all cases is a 1-mm. deviation from the base line of the activity marker on the polygraph, the range extending from +20 to −20 units. Extraneous visual and auditory stimuli were eliminated by the use of black screens and a constant masking noise.

Procedure

Habituation. For 23 consecutive days the animals were habituated to the stock and holder by means of special feeders similar to the feeder in the apparatus. They were next adapted to the movement of the food tray and of the slide in the apparatus itself. Feeding schedules were arranged so that at the start of each experimental session the animals had been deprived of food for 22 hr. Wet mash was used as food throughout the experiment and was always present in the food tray of the apparatus so that the presence or absence of the odor of food would not serve as a discriminative stimulus to approach or to withdraw.

Approach conditioning. The regular training series was begun, on the day following the conclusion of preliminary training, with the presentation of the positive CS followed by the forward movement of the slide and presentation of food in the food tray. Each animal was given 20 trials per day for five days, 22 trials on the sixth and seventh days, and 23 trials on the eighth and ninth days. Twenty trials were given on the tenth day, and the record of these trials, 191 to 210, was used in the calculations of the approach gradient.

A trial consisted of (*a*) presentation of the CS, (*b*) forward movement of the slide, (*c*) presentation of the food tray for 5 sec., and (*d*) backward movement of the slide, with removal of the food tray and termination of the CS. After 30 sec. the next trial was begun.

On the first day the forward movement of the slide was started at the same time the CS was presented. Thereafter a delay period was introduced and gradually increased so that from the sixth through the tenth days there was a 10-sec. delay period. This provided the period of time during which measurements were taken of the animals' movements for calculations of the approach gradient. From the continuous record of the animal's activity, measurements were taken of each animal's position at five points in the 10-sec. interval. These points were: 0.0 sec., i.e., the beginning point, 2.5 sec., 5.0 sec., 7.5 sec., and 10.0 sec., i.e., just before the forward movement of the slide.

Approach-avoidance training. On the day following the conclusion of positive conditioning the animals were given 20 avoidance conditioning trials with no delay period. Thereafter positive and negative trials were presented in blocks of five trials so that over the period of differentiation training equal numbers of each were presented. Twenty trials were given each day, and the first block each day was varied from positive to negative in a random manner. There was a 10-sec. delay period between presentation of the CS and movement of the slide on all trials after the first day. On each trial in which the negative CS was presented, the animal was given mild shock unless *S* pulled the stock backward, breaking the shock circuit.

A criterion of differentiation independent of the animals' behavior *after* the food or shock was presented was stated in terms of appropriate forward and backward movements during the 10-sec. interval when the CS alone was present. If the animal pressed forward against the stock, moving the activity marker more than one unit during the delay period on the positive trials, *S* was considered to have made the correct response. If it made no forward movements of one unit or more during the delay period on the negative trials, *S* was considered to have made the correct response. From the binomial expansion it may be calculated that for the animals to make the correct response eight times out of ten would occur by chance less than 5 per cent of the time. This was chosen as the criterion of differentiation.

Conflict. The conflict phase of the experiment was begun for each animal on the day following its meeting of the criterion of differentiation. The actual conflict situation was preceded by five approach trials and five avoidance trials, in that order. Thereafter, both CS were presented simultaneously on each trial, constituting an approach-avoidance conflict situation. Measurements of each animal's activity in this situation were obtained. Food or shock, as scheduled, was presented on each of the ten preliminary trials, but neither food nor shock was given on any of the conflict trials. Conflict trials were continued until the animal met a criterion of extinction of neither approach nor avoidance movements of one unit or more of the activity marker during the delay period on five successive trials. On the following day spontaneous recovery was measured by repeating the conflict conditions with the exception of the ten preliminary trials, which were omitted.

RESULTS

Approach conditioning. The average positions of the animals at the five measured points during the delay period on trials 191 to 210 are 3.38, 3.64, 5.36, 6.76, and 9.10. These values make up the composite curve (see Fig. 2). All the deviations from the base line in the composite curve are in a forward direction and become progressively larger throughout the interval. An analysis of variance was made, yielding F ratios which are significant beyond the .01 level of confidence both for the variance due to the time factor and for variance among animals. Examination of the data reveals that the *form* of the individual curves is, in general, quite similar. The differences among animals lie mainly in the relative position of the entire curves with respect to the base line.

Application of *t* tests to these data shows that, of the ten possible combinations of pairs of values, statistically significant differences are found between six pairs. Differences between the last point of the curve and the first three points are significant beyond the .01 level of confidence; the last point differs from the immediately preceding point at the .03 level. The next-to-last point differs from each of the first two points beyond the .01 level of confidence. These results offer support for the hypothesis of an approach gradient in a perdominantly temporal situation.

Approach-avoidance training. On the day the criterion of differentiation was met, the average positions of the animals at the five points in the 10-sec. interval were 4.52, 4.84, 5.10, 6.72, and 12.74. The composite curves are presented in Figure 3.

As in the case of the original approach gradient, an analysis of variance was performed and the *t* test applied to both sets of data. The analysis for the approach data yields an *F* value for "tiem" which is significant beyond the .01 level of confidence and an *F* value for "animals" that falls just within the .05 level of confidence. Again, the *forms* of the individual curves are very similar and the differences among animals lie mainly in the relative position of the entire gradients with respect to the base line. The *t* tests show that the differences between three of the ten combinations of pairs of points are significant beyond the .02 level of confidence. These are the differences between the last point when paired with each of the first three points. The approach gradient has flattened out in the early stages and rises more sharply near the end of the time interval, as compared with the approach gradient at the end of approach training (see Fig. 2). These findings offer additional support for the hypothesis of an approach gradient in a predominantly temporal situation, but point out that the form of the gradient changes following differentiation training.

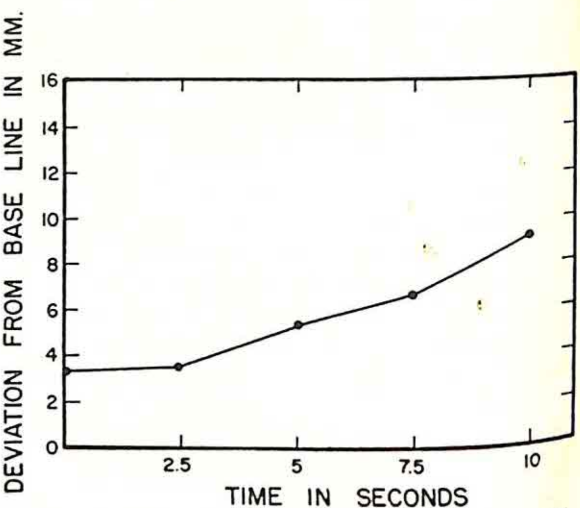

FIG. 2. Composite approach gradient—trials 191 to 210

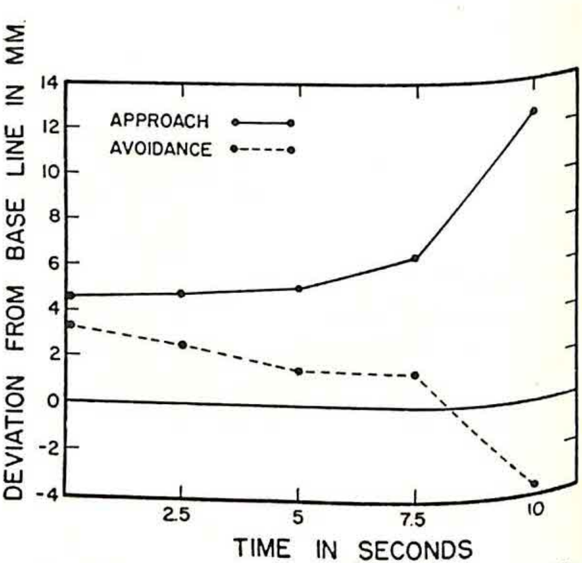

FIG. 3. Composite approach and avoidance gradients after differentiation training

The composite avoidance curve obtained at the end of differentiation training is also relatively flat during the early part of the interval, with a sharp drop after the fourth point. The average positions of the animals at the five measured points were 3.26, 2.68, 1.60, 1.58, and −3.60. Similar to the approach gradient, the *t* tests show that the differences between the last point and each of the first four points of the gradient are significant beyond the .01 level of confidence. The results from the analysis of variance suggest that the time factor is the more important variable, with the *F* value for "time" significant beyond the .01 level, while the *F* value for "animals" does not reach the .05 level of confidence. These findings offer support for the hypothesis of an avoidance gradient in a predominantly temporal situation.

It will be noted in Figure 3 that the approach and avoidance gradients do not start at the same point; i.e., the animals were holding the stock farther forward at the beginning of the approach trials than at the beginning of the avoidance trials. This appears to be a function of presenting the positive and negative trials in blocks. The records indicate that, in general, the animals tended to maintain a between-trials position farther forward as each block of approach trials progressed, and farther back as each block of avoidance trials progressed.

The tendency to approach at each of the measured points of the approach gradient was calculated by finding the difference between the numerical value at the base-line point (0.0 sec.) and the numerical value at each of the other points. The tendency to withdraw was calculated in the same manner. On the assumption made earlier by Hovland and Sears (5) and by Hull (6) that these tendencies summate algebraically, the net tendency to approach or to withdraw at any point was obtained by finding the difference between the approach and withdrawal tendencies at that point. The two gradients are strikingly similar, and the resulting net tendencies to approach and avoid are very small. They do not reach statistical significance. Prediction of behavior based on these gradients indicates vacillation and blocking throughout the entire delay period if both CS are presented simultaneously.

Conflict. The average positions of the individual animals at the five measured points during the conflict trials are shown in Figure 4. In no case do the resulting curves resemble either the approach or avoidance gradients obtained at the end of differentiation training.

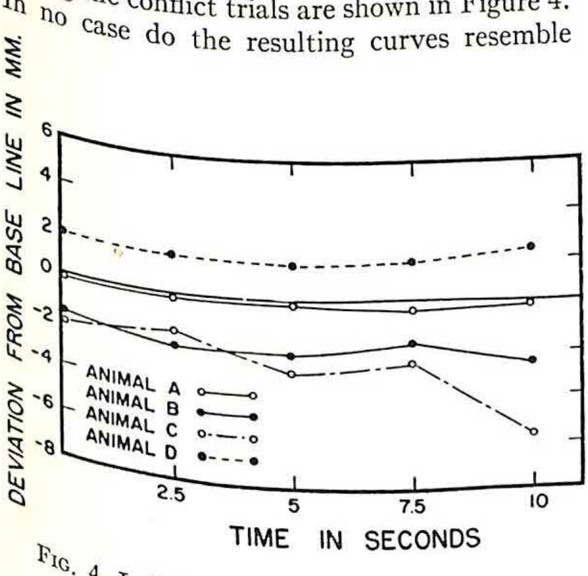

FIG. 4. Individual gradients in conflict situation

Animals A and D sat almost motionless throughout the entire delay period of the conflict trials and met the criterion of extinction in eight and nine trials, respectively. This minimized activity might appear to indicate that no conflict was involved and that extinction is the only principle needed to account for the behavior. However, the fact that the animals sat almost motionless on the first conflict trials as well as on the later trials is not adequately accounted for by the principle of extinction alone. It seems more likely that the lack of activity on these first trials can be ascribed to blocking in the presence of two opposed action tendencies. This behavior persisted throughout the entire delay period and is in agreement with the prediction made from the previously obtained approach and avoidance gradients.

In contrast to the animals mentioned above, animals B and C displayed a great deal of activity in the conflict situation, culminating in escape from the apparatus. Animal B escaped just after the seventeenth conflict trial, and animal C after only six conflict trials. On the following day these two animals were again placed in the conflict situation in exactly the same manner as the first time. Although they responded appropriately on the preliminary trials after the first presentation of food or shock, they both sat almost motionless during the conflict trials. Animal B met the criterion of extinction on the first five trials, and animal C met the criterion after eight trials. The reasoning previously applied in the case of animals A and D appears to hold for this behavior also.

Spontaneous recovery in the conflict situation was checked in each animal on the day following its meeting the criterion of extinction. In all cases the animals sat almost motionless throughout the entire session. Animal A met the criterion in seven conflict trials, animal B in six trials, animal C in seven trials, and animal D in ten trials.

DISCUSSION

In comparing the results of this study with theoretical analyses and with results obtained from other experiments, it should be kept in mind that the present data apply only to competition between approach and avoidance tendencies. Thus, in regard to Lewin's analysis (7), comparison can be made only with his Type II conflict situation; i.e., the organism faces something that has both positive and negative valence. The results of this study furnish indirect support for Lewin's postulated solution of "withdrawal from the field," and are in agreement with the results found by Hovland and Sears (5) in that vacillation and blocking were produced throughout the entire time interval.

With regard to Miller's (9) theoretical and experimental analysis, the results from this study offer support for the first two fundamental assumptions, i.e., that of an approach gradient and that of an avoidance gradient when applied to a predominantly temporal situation. Since the present method made possible the obtaining of measurements at five points in the gradient, additional information is available regarding the form of the curves. The results suggest that the gradients are not linear but tend to increase in slope as reinforcement approaches in time. Although Miller connected by a straight line the two points at which he had measurements, he points out that this was done solely for clarity of exposition, and no assumption or demonstration of linearity was involved.

Under the conditions of the present study, support is not offered for Miller's third assumption, i.e., that the avoidance gradient is steeper than the approach gradient. The two composite gradients obtained here were nearly identical in form at the conclusion of differentiation training. The behavior of the individual *S*s in the conflict situation also fails to support this assumption. If the avoidance gradient were steeper than the approach gradient and if they crossed within the limits of the experimental situation, one would expect, in the conflict phase, approach movements during the first part of the 10-sec. interval, vacillation and blocking near the middle of the interval, and avoidance movements during the last part. Examination of Figure 4 shows that this was not the case. It should be noted that Miller's deduction based on this assumption referred only to situations in which the organism has sufficient time and space to approach and withdraw without restraint. These conditions did not prevail in the present experiment. As a result, the findings are not interpreted as a refutation of Miller's third assumption. Under the present experimental conditions the approach and avoidance tendencies were nearly identical and would lead to the prediction of vacillation and blocking throughout the entire interval during the conflict phase. In general, the results support this deduction.

Hull (6), in his attempt to quantify the relationship between strength of excitatory tendency and distance from point of reinforcement, points out that there is some evidence which suggests that the relationship is logarithmic for the approach gradient. Although no study of the avoidance gradient had been made at that time, Hull suggested that it would show at least positive acceleration. In the present study both gradients show positive acceleration. Hull further proposed that when the many possibilities of variation are considered, it seems very likely that the form of the gradient, as well as the height, will undergo progressive and independent change. Support for this suggestion is found in the present study.

SUMMARY AND CONCLUSIONS

The present study was designed (*a*) to examine in a predominantly temporal situation the first three of Miller's four fundamental assumptions regarding approach and avoidance gradients in situations which are primarily spatial, and (*b*) to study the *S*s' behavior in a predominantly temporal conflict situation. The apparatus used was that devised by Bijou in his development of a conditioning methodology for studying conflict behavior in the white rat. Four male albino rats were conditioned with a procedure which presented a light with food and a buzzer with mild electric shock. The *S*s could obtain food by pressing forward in the apparatus and avoid shock by pulling backward. Measurements were taken of each *S*'s activity during the 10-sec. period that intervened between onset of the CS and presentation of the food or shock. After the appropriate responses were well established, an approach-avoidance conflict situation was arranged by presenting both CS simultaneously.

Although the small number of *S*s used in this study precludes the possibility of conclusive statements, the results suggest the following:

1. Support is given to the hypothesis of the

existence of an approach gradient in a predominantly temporal situation.

2. Support is also given to the hypothesis of the existence of an avoidance gradient in a predominantly temporal situation.

3. The slope of these gradients tends to increase as positive or negative reinforcement approaches in time.

4. The results emphasize that such gradients are not stable. In this study the form of the approach gradient changed significantly during the approach-avoidance training.

5. Under the conditions of the present study the avoidance gradient was not steeper than the approach gradient. Instead, the approach and avoidance tendencies were nearly identical at each of the measured points. From such gradients one would predict vacillation and/or blocking throughout the conflict situation. In general, the results support this prediction.

6. Spontaneous recovery of conflict behavior after extinction was minimal.

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Received April 18, 1953.

DESIGN AND RELIABILITY OF A NEW ACTIVITY-RECORDING DEVICE

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The main purpose of the present paper is to describe the design and reliability of a new device for recording spontaneous activity in rats. A related purpose is to discuss methods of determining the reliability of activity measures and to indicate an appropriate statistical method to be used in place of the usual correlation coefficients.

DESIGN

The basic recording unit consists of a cylindrical wire mesh cage balanced on a central pivot. The individual cage is 9 in. in diameter and 12 in. high. It rests in an aluminum cake pan which in turn is mounted on the central pivot. The central pivot is a machine screw 2½ in. long mounted in the center of a piece of ½-in. plywood cut in a 12-in. by 12-in. square. The cake pan also rests on four sensitive microswitches placed 90° apart around the edges of the plywood base. The cake pan can tip about ⅛ in. in any direction as the animal moves about on the floor, and the microswitches are so wired that any movement of the rat from one quadrant to another causes an electromagnetic counter to advance. In addition, any violent movements such as climbing vigorously on the wire mesh walls are recorded if they tilt the cage enough to activate the counter. Thus, minor movements that lack either vigor or extent are not recorded. This characteristic of the apparatus is further enhanced by an aluminum cookie cutter mounted upside down in the center of the cage floor. The cookie cutter prevents the animal from sitting in the middle of the cage floor and advancing the counter with minor shifts in position.

The essential details of the activity unit are represented in Figure 1. On the left is the plywood base with the four microswitches and the central pivot. On the right is the wire mesh cage resting in the aluminum cake pan. The pan normally contains a layer of sawdust to collect droppings. Also shown in the diagram is a sawed-off aluminum funnel through which food can be dropped into the cookie cutter, which serves as a food tray.

It should be noted that the present activity-recording device requires virtually no adaptation period. Studies with the apparatus show that adaptation is about complete at the end of 24 hr. and that by the end of the second day there is no further change in the animal's base line of activity unless experimental conditions are introduced. This is in contrast to the commonly used activity wheel, which is reported to require from two to three weeks of adaptation (1).

In a current series of studies (e.g., 2) at Yale University six of these units have been installed in a soundproofed cabinet. The cabinet is constructed of ½-in. plywood lined with Cellotex to minimize external sound stimuli. The six cages are arranged in two banks of three cages each, and the banks are separated from each other by an air space. This arrangement permits differential treatment of the two banks.

The cabinet with the six units is shown in Figure 2. In the photograph the cabinet doors are open to show the cages and the interior of the cabinet; in normal operation the plywood-Cellotex doors are closed and ventilation is supplied by an 8-in. fan which draws air from both banks and exhausts it through a common vent.

RELIABILITY

In the past, reliabilities of measuring instruments have generally been determined by correlating the day-to-day scores of the same animals in the same activity units. Extremely high reliabilities have been obtained with this technique. Such high reliabilities, however, may be due to differences in sensitivity between individual units. If the units vary considerably in sensitivity (e.g., differential braking in the case of activity wheels), a high reliability is insured even if the animals are very inconsistent in their day-to-day performance. This difficulty has been noted by Reed (3), who points out that these high correlation coefficients are lowered when the animals are rotated systematically from cage to cage and an average reliability is calculated.

In addition to the variance produced by differences between activity units, the reliability, as measured by correlation coefficients,, is greatly influenced by the degree of heterogeneity of the animals used. Thus the reliability obtained from a homogeneous group would be low compared with the r obtained from a heterogeneous group. This was strikingly demonstrated with the present apparatus by comparing the reliability coefficient of a homogeneous group with a group deliberately made heterogeneous by starving half the *Ss* and leaving the other half satiated. In this experiment one group of six naive Wistar rats was assigned

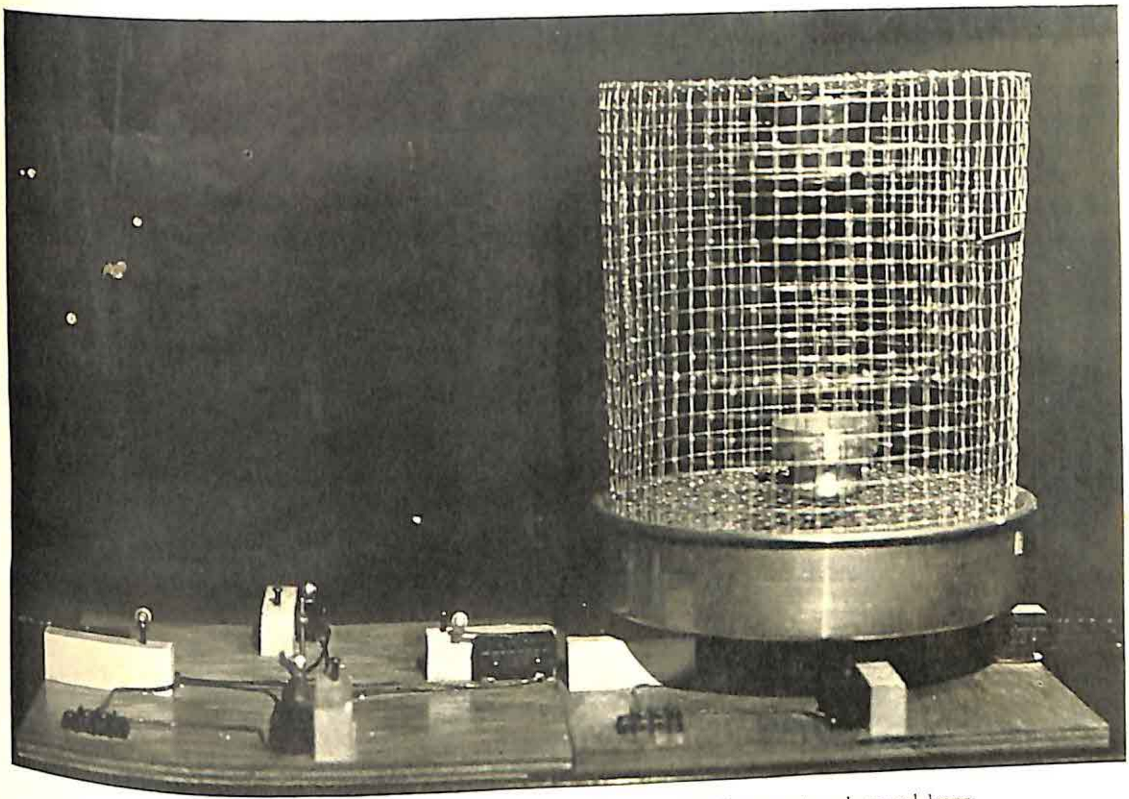

FIG. 1 Photograph of an individual activity cage and seperate plywood base

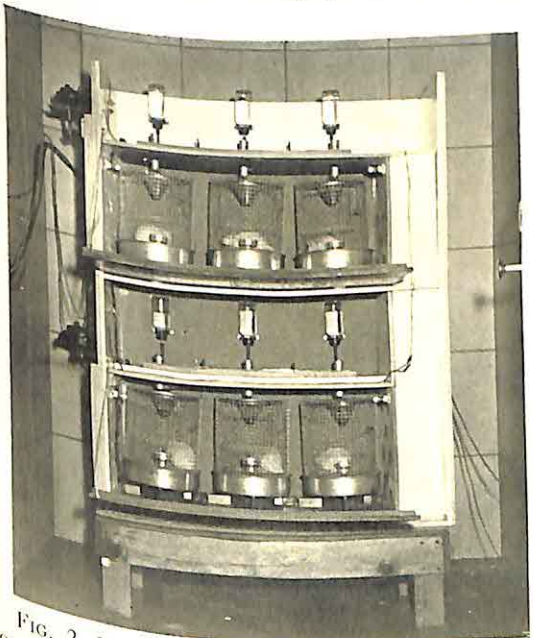

FIG. 2. Photograph of the sound-shielded cabinet containing six activity-recording units

randomly to the six activity cages and allowed to adapt to the cages for three days. Food and water were present at all times during the experiment. This group was the "homogeneous" group. In a second group of six animals, three were placed on a relatively severe deprivation diet consisting of 10 gm. (dry weight) of Purina mash per day, while the other three were kept on the same satiation diet as the first group. This group was thus the "heterogeneous" group. Beginning on the fourth day both groups of six animals were systematically shifted from cage to cage so that each animal spent one 24-hr. period in each of the six cages.

TABLE 1

Analysis of Variance for Reliability Study

SOURCE OF VARIATION	*df*	HOMOGENEOUS GROUP		HETEROGENEOUS GROUP	
		Mean Square	*F**	Mean Square	*F**
Cages	5	93,415	2.16	85,416	2.58
Animals	5	204,510	4.74	2,000,578	60.59
Days	5	145,268	3.37	75,551	2.28
Error	20	43,156		33,149	

* *F* of 2.71 needed for significance at the .05 level of confidence.

The average reliability coefficient (Pearson *r*) for the homogeneous group was +.26, whereas the reliability coefficient for the heterogeneous group was +.90. Obviously, if a similar experiment had been conducted using homogeneous animals kept in the same cages and varying, instead, the heterogeneity of cage sensitivity, similar results would have been obtained. That is, if the conventional procedure of calculating correlation coefficients from the animal's day-to-day score in the same unit is used, the resulting r would be increased by *any* heterogeneity among animals or among units.

Probably the most meaningful way of describing the reliability of an activity-recording device is to break down the scores into variance due to consistent cage differences, variance due to consistent individual differences in *Ss*, and variance due to those day-to-day fluctuations which affect all animals. Such an analysis was made of the data from the experiment just described. The results of the analysis are summarized in Table 1.

It is obvious from Table 1 that individual differences among animals account for the major share of the variance in the heterogeneous group, whereas individual differences in the homogeneous group are much less important. The mean squares for daily variations and cage variations are quite small, and neither is important when compared with the effect produced by differential feeding in the heterogeneous group. This type of analysis does not produce a single numerical index of reliability; it does, however, provide a useful breakdown of all sources of variability, which are commonly confounded in the correlation index.

SUMMARY

A new activity-recording device for rats, consisting basically of a wire mesh cage balanced on a central pivot, is described. In addition, two groups of six animals were run in a reliability study using six of the activity-recording units, and a breakdown is shown of variability due to unit differences, variability due to animal differences, and variability due to daily fluctuation. Reasons were given to believe that high correlation coefficients can be obtained only when there is considerable heterogeneity in the *Ss* used or when there is a lack of uniformity in the characteristics of individual recording units.

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Received March 16, 1953.

THE PREPARATION OF SOLUTIONS FOR RESEARCH IN CHEMORECEPTION AND FOOD ACCEPTANCE

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The need for uniformity and precision in the preparation and specification of solutions is felt in two related fields of psychological research: that of chemoreception and that of food acceptance.

In February, 1951, a symposium on chemoreception was held at The Johns Hopkins University under the auspices of the Office of Naval Research.[1] Workers in the field of chemoreception utilized this opportunity to assess the state of knowledge of this branch of sensory physiology and psychology and to discuss the direction in which future endeavor might most profitably be pointed. The group considered, among other items, the question of standardizing research methodology in this field. Although in most instances standardization was regarded as premature, there was one point on which a positive recommendation seemed indicated. This concerned the manner of specifying the taste stimulus and the stimulus magnitude.

It was originally hoped that a simple, straightforward method could be found that was acceptable to all, but correspondence with other psychologists revealed that the problem is not a simple one. Most workers on the sense of taste per se wished to rely upon molar concentrations since specification of molarity is readily interpretable within the framework of physics and chemistry. Others, however, concerned with the analysis of appetite, palatability, and related problems, have desired a simple and direct method of specifying the intake of both solvent and solute, since it is not always clear which aspect of a solution instigates ingestive behavior, the solute or solvent, or how they interact in the regulation of the feeding process. There is thus an unfortunate lack of uniformity in the specification of concentration of solutions.

Concentration is defined in *Van Nostrand's Scientific Encyclopedia* (1947) as the "amount of a given substance in a stated weight or volume of material." From the point of view of chemistry, the use of molarity, i.e., molar concentration, is the most satisfactory. The *molar* concentration is defined as the number of gram-molecular weights of a substance in one liter of solution. A gram-molecular weight is a weight in grams equal to the molecular weight of the substance in question. It should be apparent that in order to use such a nomenclature one must know the exact chemical character of the substance being used. Another less generally used term is the *molal* concentration in which specific quantities of a substance are dissolved in 1000 gm. of solvent.

There are a good many theoretical as well as practical advantages to the use of *molar* units. The first and most basic advantage is that it is a concentration unit directly related to the number of molecules in a solution. Equimolar solutions contain equal numbers of molecules. Threshold values stated in molar units are immediately interpretable in numbers of molecules. This is especially important when comparing thresholds for different substances. Further, the conversion to normality, activity, and other physicochemical characteristics can be made readily by reference to standard tables. Molarities tell what osmotic factors are operating. They automatically tell the reader what chemical was used and how the solution was made. Results stated in molarities can be readily tied in with molecular structure and activity even if no one molecular theory of taste stands correct today.

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[1] The part of this article that deals with chemoreception is a report prepared under projects NR 140721 and NR 140909 between Brown University and Johns Hopkins University, respectively, and the Office of Naval Research, Department of the Navy. The opinions expressed in this paper are not to be construed as reflecting the official views of the Navy Department.

Despite the advantages of molar units for research in the field of chemoreception, many psychologists and biologists prepare and specify solutions in terms of *percentage concentration*. In the case of food acceptance research the specification of intake in terms of grams or cubic centimeters of solution ingested is fully adequate for many purposes without conversion to molar concentration. Percentage concentrations, however, suffer from the disadvantage that a given percentage can mean different things, and it is not always clear what is meant. To illustrate the nature of the difficulty, we will describe three methods of preparing a 10 per cent solution of sucrose.

According to the first method, *E* weighs 10 gm. of sucrose and dissolves this in 90 gm. of distilled water. The total solution, whatever its volume, weighs 100 gm. Now if a rat ingests n grams of this solution, we can be sure that it has ingested $10n/100$ gm. of sucrose and $90n/100$ gm. of H_2O, where *all measures* are made and expressed *in grams*. This method of preparing a solution is known as *percentage concentration by weight* of solute and solvent. The method is especially to be recommended whenever the intake of solutions is measured and recorded in gram units.

A second method of preparing a 10 per cent sucrose solution is really a misapplication of the first and it should be discouraged. According to this erroneous method, 10 gm. of sucrose are added to 100 cc. of distilled water. Since 100 cc. of H_2O weigh 100 gm., the total weight of solution equals 110 gm. The true percentage, then, is not 10 but 10/110 or 9.1. For very dilute solutions a negligible error is introduced by neglecting the total weight of the solution. For more concentrated solutions, however, a considerable error can be introduced.

In Table 1, column A shows the true percentage concentration of sucrose solutions by weight of solute and solvent. Column B shows the corresponding percentage values for the same solutions computed as grams of solute added to 100 cc. of H_2O. With higher concentrations there can be a tremendous difference.

A third, widely used method of preparing a 10 per cent sucrose solution is to weigh out 10 gm. of sucrose and to dissolve it in distilled H_2O, diluting the solution gradually until the total volume of solution equals 100 cc.

This third method has utility in experiments where fluid intake is measured in volumetric units, as is commonly done with Richter-type bottles or graduated beakers. The intake of the solute can be readily computed when the total volume of ingested fluid is known. Thus, if a rat ingests n cubic centimeters of a 10 per cent sucrose solution, $10\ n/100$ gm. of sucrose have been ingested. It is not true, however, that for every 100 cc.

TABLE 1

The Concentration of Sucrose Solutions Specified by Different Methods

A % BY WEIGHT AS GRAMS OF SUBSTANCE IN 100 gm. OF SOLUTION	B % BY WEIGHT AS GRAMS OF SUBSTANCE + 100 cc. OF H_2O	C SPECIFIC GRAVITY	D % BY WEIGHT/VOLUME AS GRAMS OF SUBSTANCE IN 100 CC. OF SOLUTION	E MOLAR CONCENTRATION $= \frac{\text{COL. D} \times 10}{\text{MOL. WEIGHT}}$
1	1.01	1.0021	1.00	.029
2	2.04	1.0060	2.01	.058
4	4.16	1.0139	4.06	.117
6	6.38	1.0219	6.13	.179
8	8.67	1.0299	8.24	.241
10	11.1	1.0381	10.4	.304
20	25.0	1.0810	21.6	.630
30	42.9	1.1270	33.8	.986
40	66.6	1.1764	47.1	1.37
50	100.	1.2296	61.5	1.79
60	150.	1.2865	77.2	2.25
70	233.	1.3472	94.3	2.75
80	400.	1.4117	112.9	3.29

Note.—Column A × Column C = Column D. This table has been adapted from the table on pp. 1729–1730 of the *Handbook of Chemistry and Physics* (2).

of solution ingested the rat has ingested 90 gm. or 90 cc. of water. The fluid intake in grams can be calculated only when the density of the solution is known. The specific gravity for many common substances can be found in tables in the *Handbook of Physics and Chemistry*. Column C of Table 1 shows the specific gravity. Each figure gives the weight in grams of 1 cc. of solution at the percentage concentration indicated.

In experiments that utilize the third method of specification it is sometimes desirable to compute the intake of water, but unless one knows the density of the solution, or the specific gravity, correct computations of water intake cannot be made. In other words, in order to compute the water intake, one must know the number of grams or cubic centimeters of water in a specified volume of solution.

Although the values shown in column D are generally referred to as *percentages*, strictly speaking this is a misnomer. We can speak of a percentage only when one and the same kind of unit is employed. The values in column A are true percentages because solute and solvent are both expressed in units of weight, but the corresponding values in column D are actually weight/volume ratios and not true percentages.

It should be noted that true percentages can be described when units of volume are used. Thus, when the solute is in liquid form, a 10 per cent solution by volume would consist of 10 cc. in 100 cc. of solution. Ethyl alcohol in water mixtures, for example, is often reported as a percentage by volume. A 50 per cent solution by volume in this case is equivalent to a 42.5 per cent concentration by weight. Gases in mixture are usually reported as percentage by volumes. Similar discrepancies, however, are possible in specifying percentages by volume as well as in specifying percentages by weight. For example, one can erroneously add 10 cc. to 100 cc. of solvent to make a 10 per cent solution.

The use of different systems for specifying concentration becomes especially confusing when it is desired to compare the results specified by one system with those specified by another. The transformation from column B to column A in Table 1 is a matter of simple arithmetic, provided we assume that distilled water was used as the solvent. But transformations between columns A and D can be made only when the specific gravity (or some other measurement of density) is known. Usually investigators do not specify the density of their solutions.

The transformation between columns D and E is a simple matter when molecular weights are known. The values in column D resemble those of the molarity system except that grams rather than gram molecular weights are employed. A conversion to molarity can be made by this equation:

$$\frac{(\text{Grams per 100 cc.}) \times 10}{\text{Mol. Weight}} = \text{Molarity}$$

The use of molar units, as we said, is well suited to studies of taste stimulation and to other basic work on chemoreception; but for studies of food acceptance a true percentage by weight of solute and solvent may be preferable, provided the intake of fluids is measured and recorded in grams. When fluid intake is recorded in volumetric units, the method illustrated in column D is convenient despite the limitations above mentioned.

Another important matter that relates to the preparation of solutions is the precise description of substances that are used. Certain substances or drugs may be available at local pharmacies or grocery shops as well as from standard chemical suppliers. Saccharin, for example, is one such compound. It is commonly available as soluble saccharin in the tablet form. Not only is this chemically contaminated by some kind of paste or "binder," but the saccharin used in such tablets is the sodium salt of saccharin. In the *Handbook of Chemistry and Physics* the name *saccharin* is reserved for the relatively insoluble form which contains no sodium. Both forms are sweet to man, yet the presence of sodium in the solution might have other physiological effects. If substances like table salt or sugar are obtained from the local grocery store, this should be indicated because of the possibility of the presence of impurities, although cane sugar from this source is said to be of the highest purity. When chemically pure agents are used, the exact chemical terms should include some reference to the particular form if several alternate forms are available, with regard to the degree of water in the crystal, optical activity, etc. Finally, if water is the solvent, it should be made clear whether tap or distilled water has been employed. Tap water differs in mineral content from locale to locale and from time to time in the same place.

In view of the above facts the authors concur in the following general recommendations for the preparation and specification of solutions to be used in psychological research:

1. It is important that substances and chemical agents employed in the preparation of solutions be identified and described as exactly as possible. If chemically pure substances are used, this should be stated; and it should be indicated whether or not distilled water is the solvent.

2. The exact procedure followed in preparing a solution should be clearly and briefly described in published reports of research in which solutions are used. For example, it should be stated that a 10 per cent sucrose solution is 10 gm. of sucrose dissolved in 90 gm. of distilled water to make 100 gm. of solution.

3. It is recommended that the editors of psychological journals make certain that every manuscript describing work with solutions contains a clear and exact statement of the method employed in preparing solutions. This would be a distinct and long-range service to the science.

4. The choice of a method for specification of concentration varies with the purpose of the investigator. In precise work upon chemoreception, molar specification is recommended. In work upon fluid intake, a true percentage concentration by weight of solute and solvent is recommended when fluid intake is measured in grams. If fluid intake is measured in volumetric units, a weight/volume ratio (grams per 100 cc. of solution) is recommended.

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Received October 27, 1953.

THE ROLE OF EXPERIENCE IN THE "SPONTANEOUS" ACTIVITY OF HUNGRY RATS[1]

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It is commonly assumed that hunger is a state which drives the hungry animal into restless "spontaneous" activity. Casual observation of hungry rats, however, gives a different picture of the effects of hunger on activity: (*a*) Left to themselves, caged hungry rats appear to sleep much of the time and do not move about restlessly. (*b*) Very hungry rats have a lowered threshold for startle to a sudden stimulus, and when awake they are more active than satiated rats only if there is variation in the external stimulation. (*c*) Hungry rats become maximally active when exposed to external stimulation which has regularly preceded feeding in the past experience of the animal.

In a previous study (2) it was shown that in a highly constant environment food deprivation for even 72 hr. produces only a very slight increase in activity compared to the increase during 10-min. periods in which the visual and auditory environment is altered. Moreover, the magnitude of the increase in activity produced by the environmental change was related to hours of deprivation in a much more pronounced way than was the so-called "spontaneous" activity. These results are in line with observations *a* and *b* above and are interpreted by the authors as evidence that hunger does not function as a stimulus to activity but instead is a state in which thresholds of normal activity responses to internal and particularly to external stimuli are lowered. The purpose of the present study was to investigate observation *c* above under controlled conditions.

METHOD

Subjects and Apparatus

The *S*s were 23 male albino rats of the Wistar strain from the Redbank Farms, New Jersey. They were about 120 days old at the start of the experiment.

The basic apparatus unit was a stabilimeter-type activity recorder described elsewhere (1) and used in the previous study (2). It involves a circular living cage resting on a central pivot about which it can tilt slightly in any direction. Movements of the rat which shake the cage or shift the center of gravity to a new quadrant are recorded on an electromagnetic counter. Six of these units were mounted in a sound-shielded cabinet located inside a soundproof room. A special feature of the apparatus relevant to the present study was an electrically operated food release mechanism which permitted dropping food directly into the activity cages. The food release could be loaded without opening the cabinet and operated at any subsequent time from outside the soundproof room.

The cabinet had interior lights and a ventilation system involving an exhaust fan normally providing a constant masking sound; turning off the exhaust fan and turning the interior lights on or off were used to produce the environmental changes associated with feeding.

Design and Procedure

Four groups of *S*s were used, two experimental and two corresponding controls. One pair of experimental and control goups (*N* equals 5 and 6, respectively) normally lived in darkness, and the stimulus change consisted of turning off the masking sound of the exhaust fan and turning on the lights; the other pair of experimental and control groups (*N* equals 6 in each) normally lived with the lights on, and the stimulus change was fan off and lights off. All members of a given group were run in the cabinet at the same time.

In all groups the animals were first put in the activity cages and starved for three days. Then for a period of four days each animal received a daily ration of 7 gm. of Purina flour and 4 gm. of white flour mixed into a mash with 11 cc. of water. During these four days the ration was divided into three pellets dropped at random times between 10 A.M. and 6 P.M. by the food release device. The purpose of this preliminary training was to guarantee that the animal would learn to find food as soon as it was dropped.

For the experimental groups this adaptation period was followed by 12 days of training. During this training the external stimulus change was presented once each day for a 5-min. period, at the end of which the daily ration was dropped as one large pellet. Activity was read from the counters at the end of each minute of the 5-min. period of stimulus change.

For the control groups the comparable 12 days consisted of the same stimulus changes at a fixed time each day but without the correlated dropping of food; instead, their daily pellet was delivered unannounced either at 1 or 2 hr. after the 5-min. test for activity.

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[1] The authors are indebted to Belver C. Griffith and Doris Kraeling for assistance in carrying out a portion of the study.

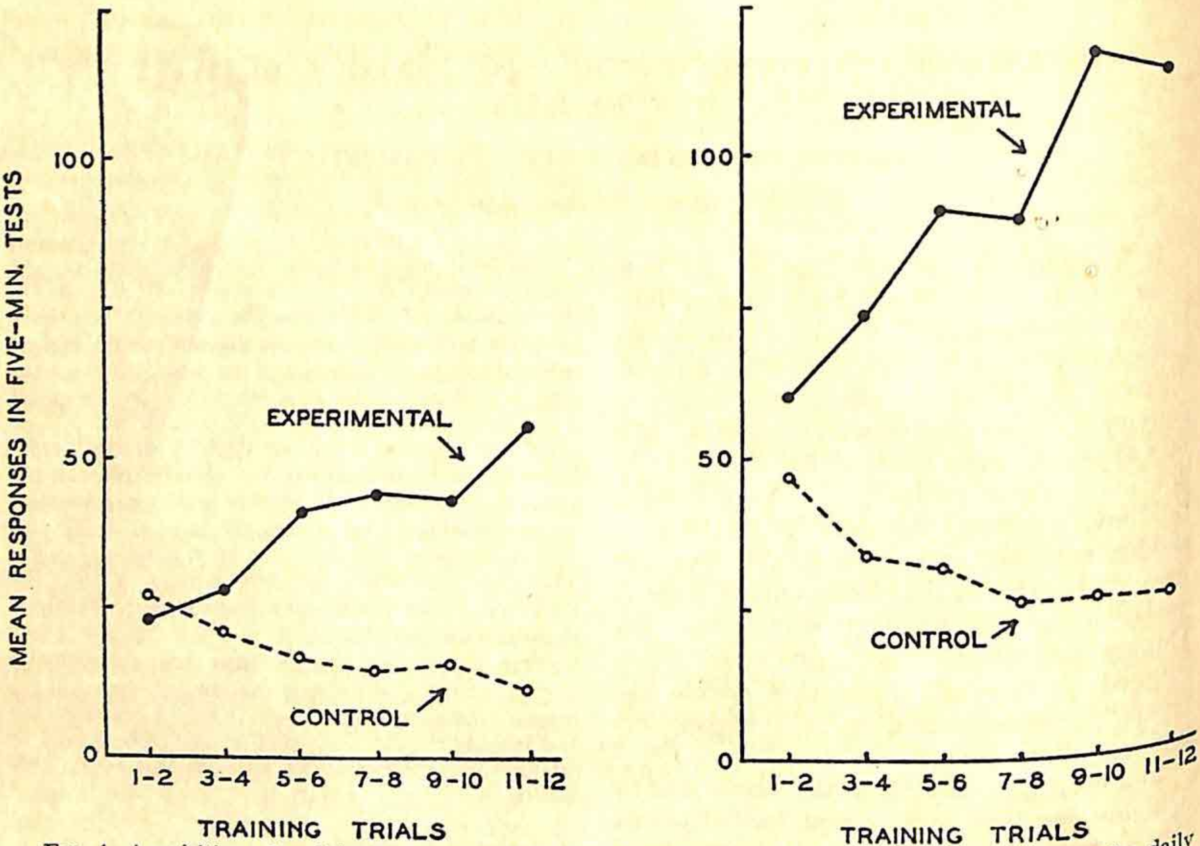

FIG. 1. Acquisition of activity in response to a 5-min. environmental change that regularly precedes daily feeding (experimental group) compared with adaptation to the change when it does not precede feeding (control group). The environmental change for the results on the left was cessation of a masking sound and a shift from darkness to light; the results on the right are with cessation of the sound and a shift from light to darkness.

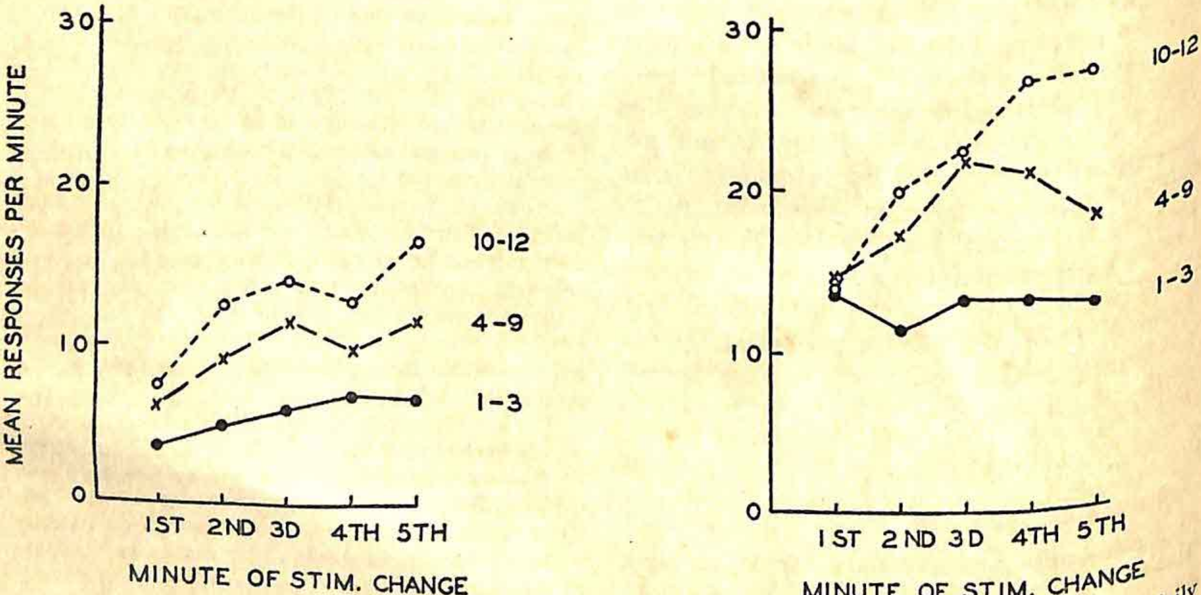

FIG. 2. Minute-by-minute activity during a 5-min. environmental change that regularly terminates in daily feeding, shown as a function of stage of training. The results on the left are for cessation of a masking sound and shift from darkness to light; those on the right are for cessation of the masking sound and shift from light to darkness. The three curves in each case plot mean performance during training trials 1 to 3, 4 to 9, and 10 to 12.

RESULTS

Acquisition of activity in response to the external cues is shown in Figure 1. The results for the fan-off, dark-to-light conditions are shown on the left; the results for the fan-off, light-to-dark conditions are shown on the right. In each case the acquisition is obvious for the experimental group compared with its control. The adaptation trends in both control groups and the acquisition in both experimental groups are all reliable beyond the .01 level of confidence.

A breakdown of the minute-by-minute activity of the two experimental groups during the 5-min. test periods as training progressed is shown in Figure 2. It can be seen that at the outset of training there is no noticeable trend through the 5-min. interval of stimulus change. At the end of the training, however, the acquired increase in activity appears most strongly in the fifth minute. Comparing the first and fifth minutes over trials 10 through 12, we find greater activity in the fifth minute (i.e., shortly before food arrived) for each of the 11 animals.

DISCUSSION

The results clearly verify the phenomenon familiar to animal caretakers and listed as casual observation *c* in the introduction, namely, hungry animals show a great deal of restless activity when cues which have regularly preceded feeding are presented. The results amplify the understanding of the relation of hunger to activity. If an observer never watched his hungry animals except when he came to feed them or use them in a food-reinforced task, he might easily conclude that hunger increases restless activity. Instead hunger per se appears to have no such effect; its effect is to augment the normal activity responses to novel stimuli and to greatly augment the activity to stimuli associated with performance of the consummatory response.

The present findings raise interesting theoretical questions about the mechanics of the acquisition which was found. The acquired response cannot properly be called "conditioned activity" because there is no unconditioned stimulus for activity in the usual sense. Hunger does not initiate activity and cannot be the unconditioned stimulus. Nor can food be regarded as the unconditioned stimulus for restless activity—it initiates eating and inhibits responses that record on the activity device.[2]

Food can, however, be regarded as the unconditioned stimulus for the consummatory response of eating, and the position taken here is that the basic learning in the present study is *the conditioning of the consummatory response to the external cue.* The restlessness may be regarded simply as a manifestation of the frustration inherent in any conditioned consummatory response. The animal cannot "consume" a conditioned stimulus or a conditioned stimulus object. If frustration is properly defined as the state that exists when drive is present and the consummatory response is stimulated but prevented from occurring, then neutral cues conditioned to a consummatory response are inevitably frustrating if they persist for any length of time.

Viewed in this light, the "acquisition" of activity found in the present study is to be interpreted, not as learning of activity, but rather as the formation of a stronger and stronger conditioned connection between the external stimulus change and the consummatory response as training progresses. The stronger this connection and the more similar the cues to those that just precede eating, the greater the frustration with cue present and goal object not yet materialized.

This interpretation has interesting ramifications when applied to maze learning based on hunger motivation. Like the external cue in the present study, the maze becomes a source of frustration as the animal gains experience with eating in the goal box. The maze cues cannot be eaten, but they quickly become conditioned stimuli for eating, especially the cues in the true paths and the cues nearest the goal box. Here, however, the animal is not caged and the excitement of delayed consummation is not manifested only in vigor of restless movements, but rather in the vigor of any movements it makes. Of all movements it can make, however, the ones that most closely lead to food will be performed with the greatest vigor because they provide cues most strongly conditioned to the consummatory response and therefore most productive of excitement up to the point of seizing and ingesting food. It may be conjectured that the animal of necessity performs correct responses more vigorously, making them prepotent over other conflicting, incorrect response tendencies.

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[2] The question may be raised as to whether or not the increase in activity produced by the environmental change is reinforced by feeding, thus accounting for the progressive rise in activity to the cues that precede feeding. This possibility has been considered and rejected on the grounds that the concept of "learning" applies to the strengthening of connections between stimulus and response and cannot explain how a learned response can be more rigorous than the response originally performed.

SUMMARY

Using stabilimeter-type activity cages, the increase in activity in hungry rats produced by a sudden change in an otherwise constant environment was recorded once each day for a 5-min. period of the environmental change. For one experimental group and one control group the environmental change consisted of shutting off a masking sound and turning on lights in normally dark environment; for a second experimental group and control group the change consisted of turning off the sound and turning off the lights in a normally lighted environment. For the experimental groups the 5 min. of change in the auditory and visual fields were always followed immediately by automatic dropping of the daily food ration into the activity cages. For the control groups the change was unaccompanied by food—their daily ration was dropped at a different time.

Experimental animals showed a progressive rise over a 12-day period in the amount of activity during the 5-min. stimulus change leading to food, while control animals showed a decline over the 12 days. Also, when the activity during the 5-min. interval was plotted minute by minute in the experimental groups, it was found that the acquisition of increased activity during the last 3 days of training was greater in later portions of the interval—shortly before food arrived.

The findings are interpreted as reflecting basically the conditioning of a consummatory response to the external cues associated with feeding. The "acquisition" of activity is interpreted, not as learning, but as a correlated manifestation of the frustration necessarily produced when a consummatory response is aroused by conditioned stimuli at a time when the goal object is not immediately accessible.

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Received June 29, 1953.

RESPONSE STRENGTH AS A FUNCTION OF DRIVE LEVEL DURING TRAINING AND EXTINCTION

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Studies by S-R reinforcement theorists have led them to conclude with Hull (2) that habit strength is independent of the drive level present during training. Illustrative studies interpreted as supporting this position are those by Kendler (3), Teel (7), and Hillman, *et al.* (1), which have found that drive level during training has no influence on response strength as measured by the number of trials to reach a criterion of extinction. These studies provide little information on the effect of drive level, during training and during extinction, on other measures of response strength during extinction. The purpose of the present research, accordingly, was to study the effects of drive level on an amplitude-during-extinction as well as a trials-to-extinction measure of response strength.

METHOD

Apparatus

The apparatus consisted of a straight alley 4 ft. long connecting a starting box and a goal box. Movable doors separated the starting and goal boxes from the main portion of the alley. Microswitches mechanically depressed by the weight of the animal operated a timing circuit which recorded the time from leaving the starting box to entering the goal box. A more detailed description of this apparatus with a few modifications can be found elsewhere (6).

Subjects

The *S*s were 20 male albino rats of the Sprague-Dawley strain, approximately 100 days old at the beginning of the experiment. They were housed in individual cages in the experimental room.

Design and Procedure

The *S*s were randomly divided into two groups: one group was trained under 60 hr. of food deprivation, and the other under 12 hr. of food deprivation. The incentive was a 2-gm. food pellet, containing equal parts of Purina Chow and water, placed in a small glass dish at the end of the goal box. On the training days each *S* was given one trial, returned to its home cage, and then given a second trial approximately 1 hr. later (the time it took to run the remaining *S*s). Training consisted of two trials per week for a period of seven weeks, giving a total of 14 training trials. This distribution of trials allowed *S*s trained under 60 hr. of food deprivation time to regain weight through 4½ days of ad libitum feeding before the next deprivation period was begun.

For the extinction trials, each of the original groups was divided into two subgroups on the basis of the individual *S*'s median running time for the last three training trials. The four resulting subgroups were: (*a*) High-High, trained under 60 hr. of deprivation and extinguished under 60 hr. of deprivation; (*b*) High-Low, trained under 60 hr. of deprivation and extinguished under 12 hr. of deprivation; (*c*) Low-Low, trained under 12 hr. of deprivation and extinguished under 12 hr. of deprivation; (*d*) Low-High, trained under 12 hr. of deprivation and extinguished under 60 hr. of deprivation. Extinction trials were identical with training trials except for the absence of food in the glass dish. Extinction trials for a given *S* continued until it met the criterion of extinction, which was three successive trials that exceeded 20 sec.

Two measures of the animal's behavior were taken: (*a*) running speed (obtained by multiplying the reciprocal of the time from start box to goal box by 100), and (*b*) the number of trials required to reach the extinction criterion of three successive running times of 20 sec. or more.

RESULTS

The main results are shown in Figure 1. This figure shows the running speeds of the four subgroups during the first ten extinction trials. It indicates clearly that drive level during training has a marked effect on the animal's performance during the early extinction trials. Table 1 presents an analysis of variance calculated from mean running speeds during the first six extinction trials, where the differences are most marked. It can be seen that the variance attributable to drive level during training is significant ($p < .05$), whereas the variances due to drive level during extinction and the interaction are not significant.

An analysis of the resistance-to-extinction data showed no significant differences between any of the four groups in the number of trials required to meet the extinction criterion of three successive trials of 20 sec. or more. An analysis of variance on these data gave F values of 0.03 for training drive level, 0.26 for extinction drive level, and 0.87 for interaction.

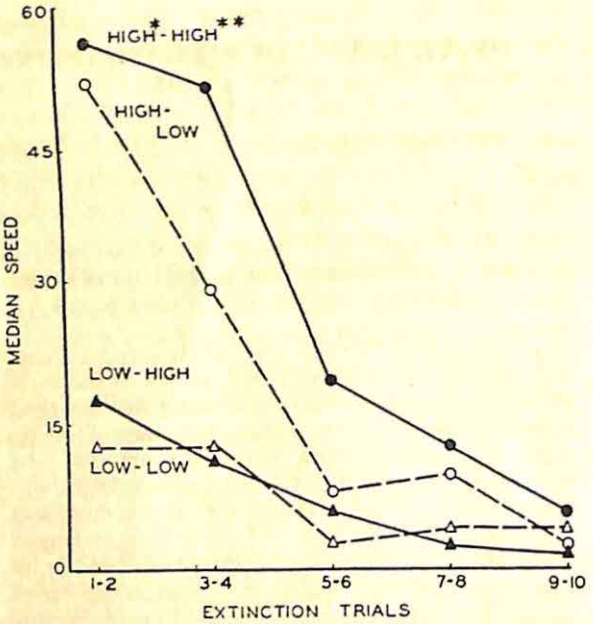

FIG. 1. Median running speeds for all groups during the first ten extinction trials. * Denotes training drive level; ** denotes extinction drive level.

TABLE 1

Analysis of Variance on Mean Speeds of the First Six Extinction Trials

SOURCE OF VARIATION	df	MEAN SQUARE	F*
Training drive level	1	1580.64	7.40
Extinction drive level	1	494.02	2.31
Interaction	1	1.25	0.01
Error	16	213.62	

* F of 4.49 needed for significance at the .05 level of confidence.

An *F* of 4.49 is needed for significance at the .05 level of confidence, indicating that none of the experimental conditions had any appreciable effect on the resistance-to-extinction measure.

DISCUSSION

The present findings are in line with other investigations (1, 3, 7) of the effect of drive level during training, if the resistance-to-extinction measure is used. That is, with this measure, training drive level has no effect on response strength. With the amplitude measure, on the other hand, there is a sizable effect in the direction of greater response strength during extinction with stronger training drive level. This effect is present regardless of the drive level during extinction.

The results seriously question Hull's (2) use of amplitude and resistance to extinction as alternative measures of reaction potential. In the present study such use would give widely disparate answers to the question of whether training drive level influences habit strength.

The results also raise questions of a more fundamental nature concerning Hull's formulation of reaction potential as a multiplicative function of drive and habit strength. Hull applies his formulation as if drive level at the time of training not only failed to influence the strength of the habit acquired, but also had no effect on the nature of the response acquired. In brief, his formulation assumes that the *same* habit is learned for all levels of drive whenever animals are trained in a particular situation. Observation of the present experimental animals, however, suggests a quite different formulation. The animals trained under conditions of high motivation appeared to learn responses which were qualitatively different from the responses learned by animals trained under low motivation. High-drive animals, for example, learned to crouch facing the starting-box door, ready to respond immediately by dashing down the runway when the door opened. Low-drive animals, in contrast, seldom exhibited this habit of "attending" to the starting-box door, and never appeared to acquire the skill of running rapidly down the alley. Thus, when drive is shifted during extinction, animals trained under low drive and extinguished under high drive do not show an immediate increase in running speed since they have not learned the responses constituting the skill of running rapidly in the experimental situation.

A problem for the above interpretation is the often reported result that an increase in drive during extinction produces a proportional increase in running speed or response rate (1, 4, 6). An explanation consistent with the present position is that such animals have either learned in the past the skills involved in rapid responding, or they learn during extinction—through high primary drive and acquired rewards provided in the experimental situation—new responses appropriate to the increased drive level.

Another theoretical factor that might be considered is that of learned drive. It might be argued, for example, that the High-Low animals in the present experiment had acquired a stronger learned drive than the Low-Low animals, and that this learned drive continues to motivate running rapidly after the primary drive is shifted to the lower level during extinction. If such a factor is actually operating, it could be subsumed under the present interpretation as another aspect of the nature of the response practiced during training.

SUMMARY

The purpose of the present experiment was to study the effect of training and extinction drive levels on response strength during extinction.

Four groups of animals were trained on a straight alley and extinguished under the following conditions of food deprivation. One group (High-High) was trained and extinguished under 60 hr. of deprivation, a second group (High-Low) was trained under 60 and extinguished under 12 hr. of deprivation, a third group (Low-Low) was trained and extinguished under 12 hr. of deprivation, and a fourth group (Low-High) was trained under 12 and extinguished under 60 hr. of deprivation.

During extinction two measures of response strength—amplitude, as measured by running speed, and resistance to extinction—were recorded. By comparing these two measures of response strength, it was found that running speed during the first six extinction trials varied directly with training drive level but did not vary significantly with extinction drive level, while the resistance-to-extinction measure was uninfluenced by either training or extinction drive level.

These results were interpreted as (*a*) seriously questioning Hull's use of amplitude and resistance to extinction as alternative measures of reaction potential, and (*b*) providing evidence against Hull's implicit assumption that animals trained under different levels of motivation learn identical habits.

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Received July 24, 1953.

SPONTANEOUS PATTERN DISCRIMINATION IN THE RAT[1]

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For the most part, pattern discrimination in animals has been studied by the use of incentives extrinsic to that provided by the problem itself. It is assumed, probably falsely, that *S* finds no joy in doing the difficult or unusual and that it will do so only in order to relieve strong hunger or thirst or to escape shock. Under such conditions, the animal is required to do two things: (*a*) perceive the difference between two or more visual forms exposed to it, and (*b*) learn to associate reward with one, punishment with another, and react accordingly. Since these two tasks are confounded, *E* is inevitably in doubt as to how well *S* can perform either one separately. The first and more important problem—ability of the animal to perceive differences—is masked by the necessity of learning a second task. It is possible, on the one hand, that a circle and a square, for example, are seen by a rat as different on first exposure; on the other hand, it is also possible that the animal must *learn* to see these figures as distinct.

From other observations, there seems little doubt that animals can show immediate discrimination of objects or forms. This is clearly shown when the indicators of discrimination are emotional or instinctive reactions released by the stimuli themselves (7). The external environment by itself does have the property of producing differential reactions on the part of an animal; furthermore, an animal will, in fact, tend to explore and manipulate its surroundings if given the opportunity. In the laboratory, Harlow and his associates (2, 3, 5) have found that monkeys will tackle, merely because they like to do so, what psychologists commonly regard as problems. Similarly, Berlyne (1) has shown that rats will explore any novel object with which they are confronted and that, of two objects (a cube and a cylinder) introduced simultaneously, the animals will spend more time exploring the one that is newer. This interesting finding suggests not only that "curiosity" can be used as a sufficient incentive for rats to make form discriminations, but also that under such motivating conditions, their ability to do so may be more readily discernible than under conventional testing conditions.

It is the purpose of the present experiment to verify and extend Berlyne's data, using curiosity as the sole motivating agent, and two-dimensional patterns as the stimuli to be discriminated.

METHOD

Animals

Forty-eight naive hooded rats, approximately 90 days old, of the McGill "bright" and "dull" strains were used. They were divided into a control and an experimental group each having 24 animals: 6 bright males, 6 dull males, 6 bright females, 6 dull females.

Apparatus

Six plywood "living boxes," 8½ by 8½ by 10 in., painted a flat black, with wire mesh tops and floors and vertically sliding doors, were constructed. The two stimulus patterns were (*a*) an inverted isosceles triangle, base 6 in., height 5½ in.; and (*b*) six vertical striations, width ½ in., height 5½ in., and ½ in. apart. The total amount of white in both patterns was equal. They were made of white paper and glued to the rear inside walls of flat black "stimulus boxes," 8½ by 8½ by 6 in., one pattern per box.

Only one side of the stimulus boxes was open, that directly opposite the pattern. Thus, by fitting the open end to the front of a living box, and then quietly removing the door of the latter, the pattern could be exposed to the *S*s.

The experiment was conducted in an air-conditioned room, 9½ by 8½ ft., lighted by two 40-w. fluorescent lamps. The living boxes and stimulus boxes were so placed in relation to the lamps during testing that approximately an equal amount of light would fall on each pattern.

Procedure

Each rat was placed in one of the living boxes, where food and water were available at all times for a 24-hr. adaptation period. Following this, each animal was tested for two 10-min. sessions as follows:

Session A. The striated stimulus pattern was presented to *S* in the manner described. After 10 min. the door of the living box was closed and the stimulus box removed for a 2-min. rest period.

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[1] This research was supported by grants from the National Research Council of Canada and the Rockefeller Foundation.

Session B. The striations were again shown to *S*s in the control group exactly as before, while the triangle was presented to *S*s in the experimental group. All other conditions during the experiment (lighting, position of living box, position of *E*) were identical for the two groups of rats.

Three measures of exploratory activity were used. *M1.* Time spent sniffing at a stimulus pattern. In the case of the striations, this was usually done by the animal in a fairly systematic manner, up one striation, down the next, and so on.

M2. Time spent actually inside (all four feet) the stimulus box.

M3. Time spent looking at a stimulus pattern; that is, the time during which a rat had its nose pointed toward a pattern, and its forepaws resting on the wooden bar separating the living box from the stimulus box.

These three measures were tested on several *S*s prior to the experiment proper and found to be serviceable. For the 24 control animals, their reliabilities (Session A × Session B) were, for M1, .57; for M2, .69; for M3, .61. All these coefficients are significant ($p < .05$).

The *E* sat quietly at the back of and slightly above the living boxes, so that all the animal's movements in relation to the pattern were plainly visible. Each measure was recorded by stop watch in seconds for every 100-sec. period.

RESULTS

The time course of exploratory activity shown by control and experimental animals is presented in Figure 1. Unlike those found by Montgomery (6) with simple mazes, the curves given by our three measures do not decline steadily with time, but rise gradually to a maximum at about 400 to 500 sec. and then fall off sharply. While the control and experimental *S*s do not differ significantly in Session A (as shown by *t* tests on each measure), they are strikingly separated in Session B, particularly in its second half.

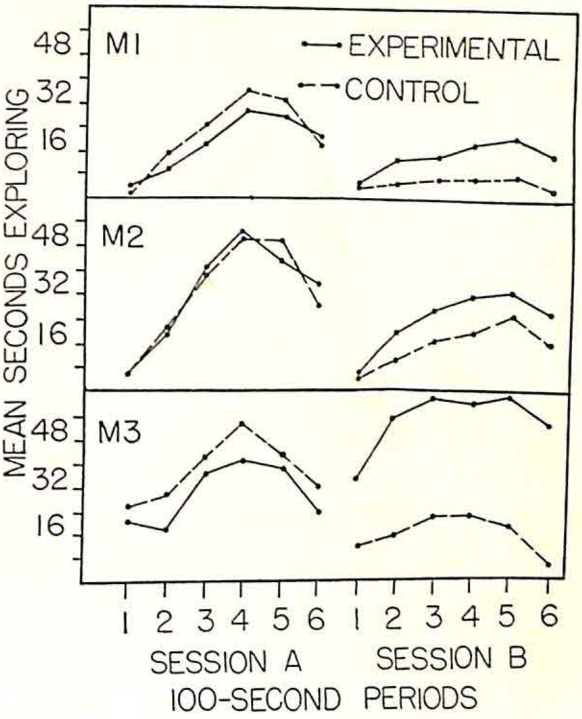

FIG. 1. The behavior of rats exploring patterns as given by three different measures, Ml, M2, and M3. In Session A both groups explored striations; in Session B control *S*s explored striations, experimental *S*s explored an inverted triangle.

In order to examine these differences statistically, two main analyses were made: (*a*) using the raw totals given by each of the three measures in Session B, and (*b*) using the log percentage changes from Session A to Session B, i.e., log (Score in Session B/Score in Session A × 100).

TABLE 1

Mean Scores in Seconds of Time Spent Exploring by Bright and Dull Rats of the Control and Experimental Groups in Two 10-Min. Sessions

MEASURE	SESSION	CONTROL GROUP		EXPERIMENTAL GROUP	
		Bright	Dull	Bright	Dull
M1	A	144.9	112.2	85.7	121.9
	B	21.0	37.4	67.0	97.3
M2	A	210.8	173.7	200.3	220.3
	B	31.4	146.8	127.3	133.4
M3	A	234.6	192.3	192.6	161.1
	B	72.6	93.1	326.8	312.8

With sex, brightness, and stimulus pattern as variables, analyses of variance were computed on *S*s' scores on each measure. Table 1 shows the mean times that bright and dull rats of the control and experimental groups spent in exploratory activity. Male and female means, since they did not differ significantly, are not represented in the table. For each measure separately, statistical results were as follows:

M1. A marked difference between control and experimental *S*s was found both with raw scores ($F = 9.47$, $p < .01$) and percentage scores ($F = 11.92$, $p < .01$). No differences appeared between male and female or between bright and dull rats.

M2. With raw scores, there were no significant differences between any of the groups on time spent in the stimulus box. However, with percentage scores, a significant difference was found between control and experimental group means ($F = 4.68$, $p < .05$), this difference being mainly within the bright group.

M3. For time spent looking at the patterns, highly significant differences were obtained between control and experimental groups, both with raw scores ($F = 32.9$, $p < .001$) and with percentage scores ($F = 16.57$, $p < .001$). No other differences appeared.

In summary, all three measures indicated clearly that experimental animals showed more exploratory activity in Session B than control *S*s.

DISCUSSION

The results presented above indicate that, given the appropriate testing conditions, rats can discriminate simple patterns spontaneously without the benefit of formal training. Two main facts should be noted. First, curiosity is a sufficient motive for the rat to solve what under other circumstances would be called a problem. The novel stimulation provided by a pattern produced exploratory behavior which characteristically rose to a maximum after about 400 to 500 sec., then declined. It could then be reinstated by the introduction of a new pattern, thus indicating discrimination. Secondly, rats who lack the benefit of previous experience with two-dimensional patterns are able to discriminate between some of them very rapidly within the 10-min. trial given. This was probably not immediate. It will be seen from the curves in Figure 1 that the greatest differences between the experimental and control groups in Session B occurred at the point where exploration was maximal for both. This suggests that some learning to a single stimulus did take place within a session. The experimental animals probably did not *immediately* perceive the second pattern as different from the first, but only after a brief inspection period.

These data indicate, in general, that an intrinsic motivation, namely, curiosity, may readily be used to demonstrate in the rat discrimination of patterns which it has never seen before. As a method, it would seem to be simpler than those using reward and punishment. As we have pointed out in the introduction, such experiments require that the animal not only perceive a difference between patterns, but also learn to associate one pattern with reward and the other with punishment. By making use of the fact that novel stimulation (a pattern) intrinsically produces a reaction (exploration) on the part of the animal, this second step is omitted. It would therefore appear to have an advantage in the study of animal perception.

Further, we would agree with Harlow (4) that there has been in psychology an overconcern with the "tissue-tension" type of motivation. Of equal, if not of more basic importance, is the type we have used here, namely, motivation dependent solely on the properties of the external environment.

SUMMARY

The purpose of the experiment was to discover if rats, motivated by curiosity alone, that is, intrinsically rather than extrinsically, could spontaneously discriminate between two-dimensional visual patterns.

Forty-eight rats of the McGill bright and dull strains were used; they were divided into two equal groups, a control and an experimental group.

A striated pattern (white on black) was first presented to animals of both groups for one 10-min. session (Session A). After a 2-min. rest period, the striations were again presented to the control animals for another 10-min. session (Session B), while the inverted triangle was presented to the experimental animals for the same length of time under otherwise identical conditions. The exploratory activity of the rats in relation to the patterns was recorded in each session by three measures.

It was found that, while the scores of the control and experimental groups did not differ significantly in Session A, they were widely separated in Session B, those of the experimental group being significantly greater.

It was concluded that (*a*) curiosity is a sufficient motivating force for rats to make simple form discriminations, and (*b*) rats without previous experience with two-dimensional white and black patterns can nevertheless discriminate between them without formal training.

These results were discussed briefly in terms of previous experimentation on rat pattern vision and in terms of contemporary views on motivation.

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Received June 19, 1953.

THE REWARD VALUE OF RUNNING ACTIVITY[1]

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A common laboratory demonstration is the running activity of rats in a Wahmann activity wheel. The rat runs along the inside rim of a drum mounted on a horizontal axis of revolution. Does the occurrence of this running response indicate a drive to be active? If so, some theorists, e.g., Miller and Dollard, would predict that the reduction of such a drive should act as a reinforcement for the acquisition of an instrumental response, since any drive reduction is considered a sufficient condition for reinforcement.

To test this prediction, ten 75-day-old male albino rats of the Sprague-Dawley strain were paired on the basis of running scores into matched experimental and control groups. They were then habituated to activity wheels which were sometimes braked so they could not rotate, and sometimes free to rotate when the rat ran. This habituation schedule and the remaining procedure were developed with an exploratory group of four pairs of rats, the results from which were similar to those reported here.

A Skinner-type bar, which the rats had previously learned in a different apparatus to press for food when hungry, was now made available in the braked wheel for a 10-min. daily session. When an experimental animal pressed this bar, both it and its control partner (which was being tested simultaneously in another wheel) were permitted to run for 30 sec. The brakes were reapplied at the end of the 30-sec. period. When the control rat pressed, the brakes were not released. After 26 of these regular reinforcement sessions, the mean number of bar presses in a 10-min. period for the experimental group was 11.5, for the control group, 7.6. Although in the expected direction, this difference is not statistically reliable.

The rats were then put on a fixed-interval intermittent reinforcement schedule. For 11 daily sessions, reinforcements were given only for the first response to occur after 0, 2½, 5, 7½, and 10 min. from the beginning of the session. Both groups now pressed the bar at a higher rate: the experimental mean for 10 min. was 31.2; the control mean was 11.4. This difference is reliable in the expected direction at better than the .05 level of confidence by a t test. The mean number of *wheel turns* for each 10-min. partial reinforcement session was 21.5 for the experimental group and 13.8 for the control. This difference is not statistically reliable.

It was concluded that the opportunity to run in an activity wheel is an adequate reinforcement for the instrumental response of bar pressing.

Received June 4, 1953.

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[1] The authors wish to thank Drs. Frank A. Beach and Neal E. Miller of Yale University for their financial support and helpful advice in the execution of this study.

STIMULI PRECEDING ELECTRIC SHOCK CAN ACQUIRE POSITIVE REINFORCING PROPERTIES[1]

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When initially neutral stimuli have been repeatedly presented just before the onset of electric shock they are sometimes described as danger signals, anxiety-producing cues, stimuli conditioned to fear reactions, or arousers of secondary motivation. Such stimuli, when subsequently presented without any shock, may or may not be expected to repress any immediately preceding behavior, much in the way that Thorndike originally supposed that punishment stamped out responses. Escape from such stimuli, however, according to the drive-reduction theory of reinforcement (10, 14, 17), is a reward which could be used subsequently to strengthen any S-R sequence.

In the two present experiments, neutral stimuli are associated with shock onset during shock periods, presumably acquiring fear-drive-arousing properties. Evidence as to other properties, such as becoming conditioned stimuli for movement or for "freezing" responses, will be available in continuous records of behavior during shock periods as well as later periods. During subsequent test periods without shock, conducted in the same apparatus so as to maximize transfer of acquired properties, these stimuli will be presented continually with certain head positions, i.e., used to punish them. The working hypothesis is that the probability of these positions and the probability of movements toward these positions will decrease because movements toward these positions are punished and/or because movements away from these positions are rewarded by termination of the danger signal and consequent reduction of fear.

EXPERIMENT I

Subjects

The *Ss* were 14 male albino rats, each weighing between 150 and 180 gm.

Apparatus

The apparatus, described elsewhere (4), consisted of one unit in which all rats were run successively.

The outer compartment was an insulated metal box into which a small ventilating fan ran continuously, maintaining the temperature at 28° to 32° C. Inside this box was a snugly fitting Quonset-shaped metal cage for the rat. The cage was clamped to a transparent floor 2 in. above the floor of the box. A slot for the neck of the rat, 1¾ in. high and ¾ in. wide, was in the front end of the cage. To prevent escape through the front slot, a bar was placed ¹⁄₁₆ in. in front of the slot and at the height of ⅞ in. With the cage placed around a rat and escape through the front slot prevented, the remaining activity of the rat consisted of occasional postural adjustments and frequent head and tail movements.

Lateral flexions of the animal's head were recorded by two photoelectric cells, one above each side of the head. Under the transparent floor, directly beneath each photocell, was a 7-w. 115-v. clear light bulb, from which most of the heat and visible light was filtered by a thin bottle of iodine solution. The sensitivity of each photoelectric unit was adjusted until rotation of a dummy rat head to a position more than 22° off center actuated the relay for that side. This relay remained on until the head came back to less than 12° off center. Each relay controlled a pen of an operation recorder, the paper chart of which was moving 1½ in. per min.

The electric shock consisted of an alternating current of 0.20 Ma. through moistened felt electrodes clipped to the tail of the rat. This current was supplied by 120 v., 60-cycle a.c. in series with 0.1 megohm protective resistance, 1.0 megohm variable resistance, and a meter with a maximum range of 0.30 Ma.

The blinking stimulus was a 5-cycle per second fluctuation in the indirect illumination. A shielded 7-w., 115-v. light bulb in the center, in front of the rat, was turned off and a motor-driven microswitch alternately lighted for 0.2 sec. each, a similar bulb on the right and then a similar bulb on the left. All bulbs were operated at approximately one half their rated voltage, providing less than 1 ft-c of illumination of the eyes of the rat.

The recorder and all relays, switches, and clock motors were in one room; the photoelectric cells and cage for the rat were in another room.

Procedure

Each rat was placed on the transparent floor and the cage was snuggled down over its body and feet. The horizontal bar was placed under the chin to prevent escape through the front of the cage. The cage was centered and then fastened to the floor. Electrodes were clipped to the tail, the photoelectric cells were swung into position over the head of the rat, and the lid of the box was closed. The fan was turned on, forcing air past the infrared light sources under the transparent floor and out of the top of the box.

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[1] Some of the data contained herein were in a paper titled "Non-Avoidance of a Stimulus Associated with Onset of Electric Shock," presented at the Symposium on Conditioned Anxiety at the MPA meeting in Chicago, 1951. Appreciation is expressed for the suggestions and encouragement of Dr. Neal E. Miller, and also for the comments of the discussants of the symposium, Drs. O. H. Mowrer and G. R. Grice.

Each rat was left in this apparatus for three adaptation periods totaling 50 min. Each rat was randomly assigned to one of two groups until a total of seven animals had been assigned to each group. During the three succeeding shock periods, shock was applied for 5 sec., once each minute for 90 min. During these shock periods, each rat was subjected to one of two treatments. The "Before" treatment consisted of blinking the illumination throughout the 1 sec. before each shock began. The "During" treatment consisted of blinking the illumination throughout the fifth and last second during each shock.

Beginning immediately after the last shock period, the blinking was tested to see if it had acquired any punishing or negatively reinforcing properties. During three 30-min. test periods between which there were two 24-hr. breaks, the photoelectric cells blinked the light as long as the rat's head was on the nonpreferred side. (The nonpreferred side for each animal is the side on which it spent the smaller amount of time during the last shock period.)

EXPERIMENT II

Subjects

The *S*s were 20 male albino rats, each weighing between 150 and 180 gm.

Apparatus

The apparatus differed from that of the earlier experiment in the following respects: (*a*) The neutral stimulus was the clicking of a 110-v. a.c. relay behind the shielding partition directly in front of the rat. The armature was padded so that the downward, but not the upward, movement produced an audible click. This relay was actuated by the same motor-driven microswitch in the adjacent room which blinked the illumination in the previous experiment. (*b*) A 30° lateral flexion of the head was required to close the photoelectric relay; return to within 22° of center opened the relay.

TABLE 1

Reinforcing Effects of a Blinking Stimulus Which Had Been Presented Before or During Shocks in Period 1

(Group means [$N = 7$] of total frequency and total duration of responses in seconds and of mean reciprocal [$\times$ 1000] of latency and mean duration per response.)

DEPENDENT VARIABLE	RESPONSE DATA FROM SUCCESSIVE 30-MIN. PERIODS								LEVEL OF CONFIDENCE FOR THESE HYPOTHESES	
	During Group				Before Group				$3 = 3$	$3 - 1 = 3 - 1$
	1	2	3	4	1	2	3	4		
Reinforced side										
Frequency	32	56	23	38	19	38	38	39		.04
1/Latency*	19	34	18	23	17	16	39	25		
Duration	72	134	42	71	43	95	325	164		.05
D/F	2.2	2.5	1.8	1.8	2.5	2.4	5.8	4.2	.07	.05
Other side										
Frequency	84	87	64	81	66	82	40	51		
Duration	503	462	215	409	377	640	59	191	.04	
D/F	.8	7	10	7	13	10	3	7		
Both sides										
Frequency	116	142	88	120	84	120	79	90		
Preference (%)	30	45	28	36	25	33	50	54		
Duration	575	596	257	480	420	735	384	355		
Preference (%)	17	36	24	29	18	24	56	57		

* Represents average quickness with which the head returned to reinforced side after leaving it. Four of the 56 scores determining this row of means were estimated by interpolation. In all other statistical computations, records of *S*s with incomplete data are discarded rather than estimated by interpolation.

Procedure

Procedure differed in the following respects:

a. There were no adaptation periods. Each rat was in the apparatus for three consecutive periods, one 30-min. shock period being followed immediately by 1 hr. (periods 2 and 3) during which stimuli were tested for negative reinforcing properties.

b. The neutral stimulus occurred either throughout the 3 sec. before each shock or during the middle 3 sec. of each shock.

c. During test periods only one half of the Before and one half of the During group received the clicking as long as the head was on the nonpreferred side. The rest were given only one click each time the head moved to the nonpreferred side and interrupted the light beam. No click was audible when the head returned to center.

d. The front feet were bound together with adhesive tape so as to reduce the extent of twistings around the longitudinal axis.

e. Data were recorded from chronoscopes and impulse counters.

RESULTS

The skewness of distributions of duration and frequency noticed in Experiment I is markedly reduced or absent in Experiment II, presumably because of item *b* under *Apparatus* and item *d* under *Procedure* above. However, in order to make analysis of the data from both experiments comparable, a nonparametric test (7 15) was applied to each, with certain levels of confidence being approximated by linear interpolation and extrapolation.

In order further to facilitate comparisons between the two experiments, the same two null hypotheses were tested in each experiment: (*a*) the Before group and the During group data from the second reinforcement period, period 3, are random samples of the same population, and (*b*) as a partial control for individual differences, the Before group and the During group changes between periods 1 and 3 represent two random samples from the same population (see the last two columns of Tables 1 and 2).

Finally, comparisons between the two experiments were simplified by pooling data from the two reinforcement procedures in Experiment II. In this experiment, reinforcement by continuous clicking during test

TABLE 2

Reinforcing Effects of a Clicking Stimulus Which Had Been Presented Before or During Shocks in Period 1

(Group means [$N = 10$] of total frequency and total duration of responses in seconds, and of mean reciprocal [× 1000] of latency and mean duration per response.)

DEPENDENT VARIABLE	RESPONSE DATA FROM SUCCESSIVE 30-MIN. PERIODS						LEVEL OF CONFIDENCE FOR THESE HYPOTHESES	
	During Group			Before Group				
	1	2	3	1	2	3	$3 = 3$	$3 - 1 = 3 - 1$
Reinforced side								
Frequency	43	14	21	40	24	43	.01	.03
1/Latency	25	8	12	23	14	20	.01	.01
Duration	45	16	13	47	37	88	.03	.02
D/F	.9	1.2	1.5	1.1	1.4	2.1		.06
Other side								
Frequency	67	33	41	70	32	56	.07	
Duration	127	99	65	87	56	117		.07
D/F	2.2	2.7	1.9	1.3	1.7	1.9		
Both sides								
Frequency	110	47	61	109	56	100		.05
Preference (%)	38	30	34	36	44	51	.07	.04
Duration	172	115	96	134	93	205	.05	.01
Preference (%)	25	24	27	31	37	51	.07	

periods produced a greater difference between Before and During groups' frequency and duration measures than reinforcement by single click. Level of confidence for interaction between training and testing procedures was .001 for the change in duration on the reinforced side, though no significance attached to similar interaction with respect to change in frequency on the reinforced side. However, even reinforcement by the single clicks indicated in both cases that learning in the Before group was greater than in the During group (although in no case was the group difference statistically significant for the small samples of five cases).

Tables 1 and 2 indicate the following differences between data for the Before and During groups. Items *a* to *d* lead to rejections of the null hypotheses and also reject them by group differences which are in the exact opposite of the direction predicted:

a. Frequency of head movements toward the reinforced side increased significantly more in the Before than in the During group.

b. The reciprocal of latency, or the average quickness with which the head returned to the reinforced side after having turned away, increased significantly more in the Before group than in the During group in Table 2, though a difference in the same direction in Table 1 is not statistically significant (see footnote in Table 1).

c. Total duration of head position on the reinforced side increased significantly more in the Before group than in the During group in both experiments. Further analysis indicates that after a log transformation of data in Table 1 the variance of the Before group increases significantly ($F = 66.0!$) between the first and the third period. In Table 2, however, such a change is not as pronounced ($F = 1.2$).

d. Group means of individual mean duration per response (D/F) on the reinforced side increased more in the Before group than in the During group.

e. Responses on the other, nonreinforced, side are in general not significantly differently affected in the Before group than in the During group.

f. Total responses to both sides increased more in the Before than in the During group. However, when a partial control for these changes in general activity is instituted by determining mean preferences for the reinforced side, i.e., mean of individual ratios of response frequency (or duration) on the reinforced side relative to response frequency (or duration) on both sides, the Before groups show an increasing preference for the reinforced side in both experiments. Although group differences in increases in preference are significant in only one out of four instances, the trends are similar in both experiments. Additional similarity between experiments is apparent when one observes that, although the design of the experiments was such that no *S* preferred the reinforced side during period 1, the following percentages of *S*s preferred the reinforced side during period 3: In Experiment I, During group, 14; Before, 57; Experiment II, During group, 10; Before, 60.

g. The following is more nearly true of the Before groups than of the During groups: Those *S*s with high relative frequency of moves toward the to-be-reinforced side during the shock period were temporarily (i.e., during period 2) influenced, presumably by the danger signal, to pause longer on the reinforced side. Net increase in duration per response (D/F) between periods 1 and 2 correlates as follows with frequency preference during period 1: In Experiment I, Before group rho equals .70, while During rho equals

−.51. In Experiment II the correlations are .10 and −.58, respectively. Three of the four correlations are statistically significantly different from zero. None of the correlations between these variables for periods 1 and 3 is significantly different from zero, however.

DISCUSSION

The results of both experiments indicate that the probability of a head movement toward a certain position, and also the total duration in that position, will increase if that position is accompanied by stimuli which had previously been associated with the onset of electric shock. This is opposed to our prediction that the animal would learn to avoid the position which aroused fear. Currently popular conceptions of secondary drive, anxiety, punishment, and repression do not appear to lead to a simple explanation of this result.

Certain alternative explanations suggest themselves. Ours might be chance results due to sampling errors. This is unlikely, however, in view of the moderate levels of confidence and the similarities of the trends in the two separate experiments.

It cannot reasonably be argued that the stimulus for the During group was in a more favorable temporal position to become a CS for fear than was the stimulus for the Before group. An earlier experiment with procedure similar to that of Experiment I (4) indicates that a blinking stimulus which had been presented throughout the third second after termination of the shock had effects which parallel those in the present During group with respect to duration and frequency of response.

Data from the reinforced side, if they were the only data obtained, could be parsimoniously explained by stating that the stimulus in the Before group had a general motivational effect on total activity rather than a specific reinforcing effect limited to reinforced responses. However, this explanation becomes complicated when data from the nonreinforced side are used in the derivation of scores which are presumably independent of total activity: relative preferences for the reinforced side. When this correction is made for changes in total activity, we find that the preference of the Before group increases, if not significantly, at least similarly in the two experiments.

Systems utilizing various concepts of reinforcement—ranging from the limited concept of need reduction (10) through the more general concept of stimulation reduction (14) to the concept of stimulus change (6, 8, 18)—suggest to the author that not only fear but also any other response elicited by shock onset will tend to become conditioned to immediately preceding stimuli. In this connection it is somewhat surprising that among the experiments in the area of secondary motivation there have been few systematic observations of overt responses elicited by the primary drive of shock (2, 11, 14, 17).

Fifty-seven per cent of the movements occurring within the first second after shock onset were movements away from center in an experiment similar to Experiment I which employed a larger number of *S*s (4). Therefore, during period 1 the stimuli before shock, e.g., the stimuli of the Before treatments, would tend slightly to become conditioned to movements away from center. During the test periods, whenever the head moved toward the reinforced side, the stimuli would occur automatically. Any away-from-center movement tendency consequently elicited by the stimulus would facilitate the amplitude and hence duration of the ongoing movement, since tendencies toward movement to the opposite side would be under reciprocal inhibition. The immediate effect of such events would be to increase duration per response (D/F) on the reinforced side, and, other things equal, to increase absolute and relative total duration on the reinforced side. An alternative path to the same expectation of the obtained increase in D/F would come from the additional observation that many movements during the first second of shock are mutually antagonistic. To this extent one would expect the stimuli of the Before treatment to arouse conflict or freezing whenever the head is on the reinforced side during the test periods. The reduced effectiveness of a momentary click relative to continual clicking is interpreted as being more consistent with the freezing hypothesis.

Furthermore, the stimuli before shock become somewhat more likely to elicit, as a CR, a movement toward the preferred side than to elicit the opposite movement. During the test periods any movement toward the reinforced side would start the signal which would stop the head movement and possibly even start a movement to the opposite, nonreinforced side. We would expect a consequent decrease in duration per response on the reinforced side.[2] That this is one of the factors in the present experiment is indicated by result *g*: The animals with the most preference for movements toward the preferred side during the shock period were the animals with the least increase in duration per response on the reinforced side during the test periods.

The tendency of a danger signal to increase the duration of positions subsequently correlated with that stimulus seems to be equally well explained by the various reinforcement theories, as long as the importance of secondary drive is minimized, but its tendency to also increase the frequency of the preceding movement and the quickness with which the head returns to the dangerous position cannot be explained by need- or drive-reduction theory without the usual *ad hoc* assumption that any action is prima-facie evidence for a motive for that action.

It is possible that the frequency and quickness of responses increased in the Before groups because the duration per response increased in these groups. This increased D/F or pause after each move toward the reinforced side would serve as reinforcement for the same reason as did temporary removal from a box (8), presenting a manipulable puzzle (9), opening a window in an experimental box (3), increasing the length[3] of a cul-de-sac (13), or increasing the vigor and duration of consummatory activity (18): The *S* would not retrace its steps, or, if it did, it would be after a sufficient delay so that some of the interoceptive and other stimulus events would have disappeared or been replaced by new stimulation and hence would have remained conditioned to the movement sequence which started the delay-producing ("reinforcing") stimulus.

SUMMARY

In each of two experiments rats were restrained in a cage and either an auditory or a visual stimulus was presented either before or during electric shock. After the last shock, the stimulus was automatically correlated with the nonpreferred head position. In both experiments, duration of this head position and also the frequency of moves to this side increased significantly more in the Before groups than in the During groups. Discussion points out difficulties in explanations utilizing concepts such as secondary drive (e.g., fear), punishment, or repression. These difficulties are not present in explanations derived from S-R contiguity theory.

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Received July 17, 1953.

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[2] For these analyses and other suggestions the author is indebted to Dr. W. K. Estes.

[3] See footnote 2.

SATIATION EFFECTS UNDER FIXED-RATIO SCHEDULES OF REINFORCEMENT[1]

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In a fixed-ratio schedule the reinforcing stimulus appears only after a fixed number of responses has been emitted. Skinner (3, p. 385) has pointed out three consequences of such a schedule:

a. The probability that a reinforcement will appear during a rapid burst of responses is high. As a result, rapid responding is selectively strengthened.

b. Rapid responding produces more frequent reinforcements. This in turn increases the rate of responding still more. A cyclic process is set up which culminates in a maximal rate.

c. The fixed number of responses becomes a discriminative occasion for reinforcement. Each successive response, as this number is approached, sets up a stronger occasion for reinforcement. This has the effect of making the behavior "self-generating." As successive responses are emitted, there is an increasing probability that the run will be completed.

Skinner has presented data illustrating these phenomena in rats (2) and pigeons (4), and has indicated the importance of ratio size and amount of reinforcement (3, pp. 103, 386). The present experiments were designed to investigate the effects of partial satiation upon food-reinforced fixed-ratio responding, and to determine whether the phenomena observed could be extended to cats and monkeys.

METHOD

Subjects

Four male Wistar rats, two male stock cats, and one female rhesus monkey served as *S*s. All animals had extensive previous experience with lever pressing on regular and fixed-ratio schedules of reinforcement.

Apparatus

Skinner boxes of sizes appropriate to the different species were used. A system of relays and timers automatically controlled the scheduling, recording, and reinforcement delivery. Responses were recorded on a Harvard Cumulative Recorder.

The cats, monkey, and two rats received liquid reinforcement. This consisted of water for the rats, a 50 per cent mixture of evaporated milk and water for the cats, and water sweetened with table sugar for the monkey. Two rats were reinforced with food pellets, .045 gm. in weight and manufactured from Purina Laboratory Chow.

Procedure

Partial satiation was accomplished first by running the animals for long sessions, during which a large number of reinforcements was secured, and second, by feeding the animals before running. The experiment was conducted in two phases. In the first phase, the liquid-reinforced rats were deprived of water for 48 hr. before running; the cats were kept at 70 per cent of their ad libitum body weight; and the monkey was deprived of food and water for 40 hr. The two food-reinforced rats received all their food in the experimental situation and were run every day. The *S*s ran for 60 to 150 hr. at various fixed ratios in phase 1.

Only the monkey and the two liquid-reinforced rats were used in the second phase. Prior to phase 2, these animals were placed on a ratio of 25 responses per reinforcement for three sessions. They were kept on this ratio for three sessions in the second phase. Immediately prior to running, the rats had access to water for ½ hr., and the monkey was fed approximately 500 cc. of the sugar solution.

RESULTS

Sample records from the first phase are presented in Figure 1 for one rat, one cat, and the monkey. The rate for a given individual is essentially two-valued, with a zero rate occasionally appearing just after a reinforcement and a high, constant rate prevailing at other times. In the case of the cat, short pauses follow each reinforcement, even at the beginning of the record. These, however, are independent of the experimental procedure, resulting from a small residue of milk around the rim of the liquid dispenser. Following each reinforcement, the cats spent 5 to 10 sec. licking this residue. With the exception of this artifact, the rates are generally regular at the start of the sessions, with breaks of varying lengths beginning to appear as the period progresses. With few exceptions these breaks appear immediately after a reinforcement. Even at the end of the session, however, when

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[1] The authors are indebted to Mr. Irving Geller for his assistance in the performance of this experiment.

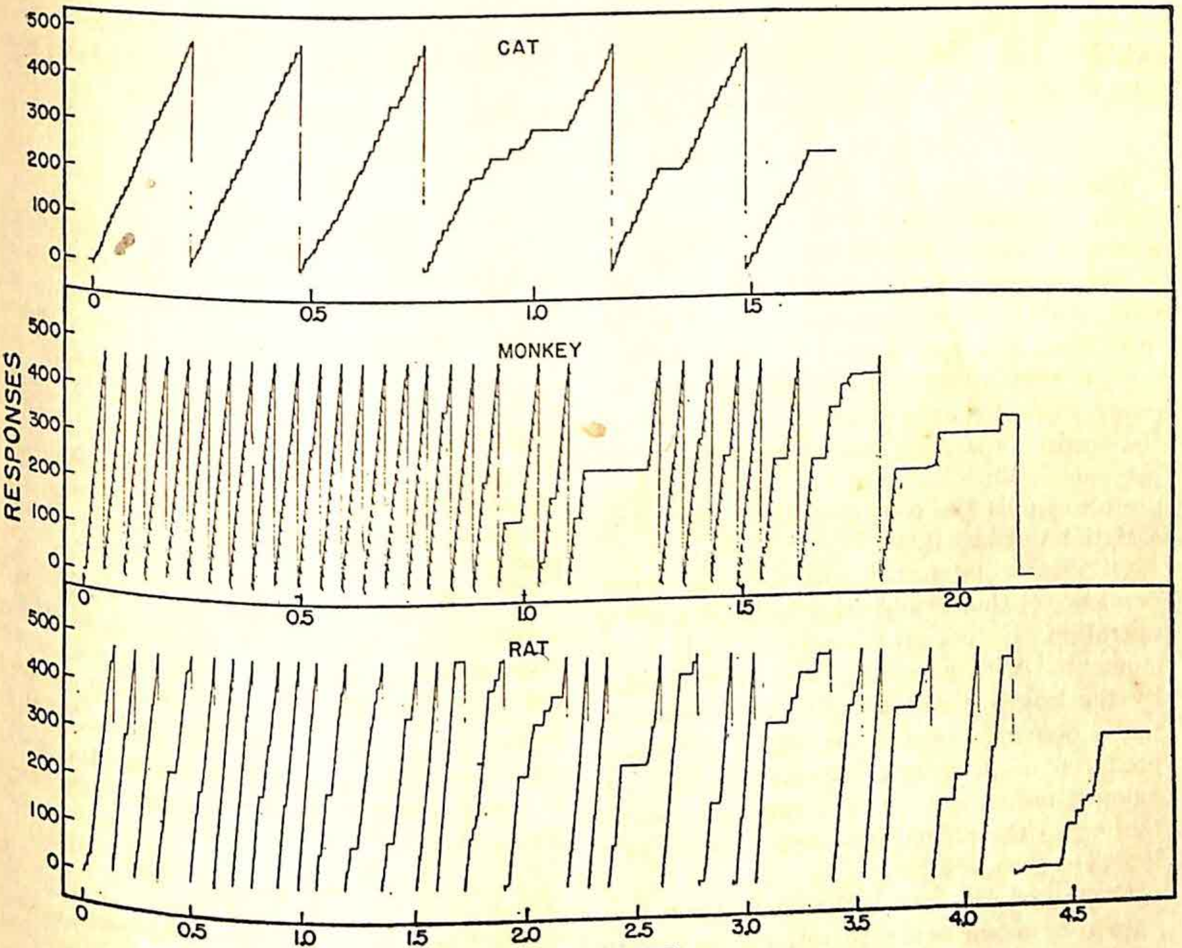

FIG. 1. Sample cumulative response records under fixed-ratio schedules of reinforcement. Ratio of responses to reinforcements is 25:1 for the rat and monkey, and 20:1 for the cat. The short diagonal strokes indicate reinforcements.

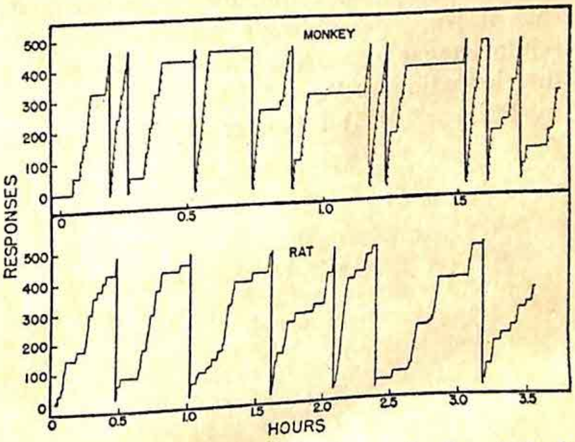

FIG. 2. Sample records following prefeeding. Animals and schedules are the same as those in Figure 1.

long periods of no responding have become frequent, the same rate is maintained when the animal does respond.

After subtracting the time taken for pauses following reinforcement, the response rate was determined over the first, middle, and last 30 min. of each session at a given schedule. This did not include the first session, during which the animal adjusted its rate from the previous schedule. The initial rate ranged from a low of 51 responses per minute for one of the rats to a high of 167.7 responses per minute for the monkey. No variation greater than 1 per cent of the initial rate was observed within or between sessions for a given animal at a given ratio.

Figure 2 shows sample records from the monkey and the same rat as in Figure 1 after they had been prefed. The only effect of the partial satiation appears to be an earlier and more frequent appearance of the periods of no responding. As a consequence, the total number of responses emitted during the experimental period is less. However, when the animals do respond, their rates are the same (within 1 per cent) as those observed at any time during the first phase.

DISCUSSION

The general features of the fixed-ratio curves are in agreement with those previously observed by Ferster and Skinner. With respect to the pauses following reinforcement, they write, "With short enough ratios—under 60 or so for the pigeon—there is no pause following the reinforcement. With larger ratios the pause increases as a function of the size of the ratio" (personal communication). The present findings indicate that these pauses are also under the control of deprivation and satiation operations.

Of greater interest, perhaps, is the independence of the response rate from the feeding operation. If total responses had only been summated with a counter, and then divided by the length of the experimental session, it would have appeared as though feeding produced a lower rate. Examination of the moment-to-moment record, however, indicates that when the animals do respond, their rate is always the same.

Connected with this is the observation that once the animal began to respond, it always continued without a break until the next reinforcement was received. When the animal responded, its own behavior set up a powerful discriminative occasion for reinforcement, each response generating a successor until the reinforcement appeared. Evidence for such a discrimination, or "count," has been presented by Skinner (4) and Ferster (1). The present data indicate that degree of satiation alters only the probability of occurrence of the first response in the run, but has no effect upon the discrimination responsible for the stable rate.

SUMMARY

Four rats, two cats, and one rhesus monkey were trained to press levers under fixed-ratio schedules of reinforcement. The effects of satiation were observed (*a*) after a considerable number of reinforcements had been received in the experimental situation and (*b*) after feeding the animals prior to running them.

Characteristics of the cumulative response curves were similar to those previously obtained by Skinner and Ferster from rats and pigeons.

The effect of satiation was to introduce periods of no responding immediately following reinforcements. However, when the animals did respond, their rates were constant and independent of the degree of satiation. Prefeeding simply produced an earlier and more frequent appearance of the periods of no responding.

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Received June 26, 1953.

THE EFFECTS OF MASSING AND DISTRIBUTION OF EXTINCTION TRIALS ON THE PERSISTENCE OF A FEAR-MOTIVATED INSTRUMENTAL RESPONSE

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Fear (anxiety) has been defined in stimulus-response terms as a conditioned pain reaction (10, 11). According to this view, if certain stimuli are associated with pain through conditioning, presentation of these stimuli in the future, unaccompanied by pain, will elicit certain components (visceral, kinesthetic, etc.) of the original pain response. As employed here, the fear response refers to a hypothetical complex of such conditioned implicit reactions.

Fear may also be considered in its capacity to act as a secondary drive. A number of experiments (6, 8, 12, 14, 15) have been performed to test the two major requirements of this point of view: fear has been shown to have the capacity to motivate new learning and, through its reduction, to act as a reinforcing state of affairs.

One of the perplexing problems arising from this kind of analysis concerns the persistence of the implicit fear response in the absence of the motivational-reward conditions (pain and its reduction) on the basis of which the fear was acquired. There are two possibilities: (*a*) The implicit fear response may extinguish with nonreinforcement, just as fear-motivated responses and other responses do. (*b*) The implicit fear response may persist, while only the fear-motivated response is extinguished. In this connection, it has been suggested that during the nonreinforced trials the reduction of fear occurs in such close temporal proximity to the visceral and kinesthetic components of the implicit fear response that it serves to reinforce their occurrence. Fear reduction would also serve to reinforce the fear-motivated behavior; but if the overt behavior results in the development of much reactive inhibition and the implicit responses do not, the fear-motivated response might be expected to extinguish more rapidly than the fear response itself.

Some data on extinction of fear are available. Mowrer (12) and Estes (2) have shown that an avoidance response based on conditioned noxious stimulation will extinguish when the noxious stimulus is consistently withheld. Having established a fear response with shock stimulation in an avoidance training setup, Miller (7) reported that the fear-motivated response persisted during a long series of nonshock trials, but eventually began to extinguish. May (6) demonstrated extinction and spontaneous recovery of a fear-motivated avoidance response. These data suggest, in the main, that fear-motivated responses, as distinguished from fear responses, eventually extinguish in the absence of primary reinforcement. In all cases the extinction trials were relatively massed. Some of the results, which show spontaneous recovery of this response after a period of rest, suggest that no real "forgetting" of the fear has occurred, but, rather, that the overt response is temporarily suppressed by some kind of work-inhibition factor. This work could be in the overt response, in the implicit fear response, or in both. It is possible that if a high degree of distribution of trials were employed in an experimental situation, a fear-motivated response, once established, might be shown to persist with little diminution. If this were found, and no other motivational-reward condition could be identified in the situation, we would have evidence that the implicit fear motivation itself has not diminished appreciably.

STATEMENT OF PROBLEM

If it is postulated that (*a*) response strength is some joint multiplicative function of habit strength and drive, as Hull (3) does; (*b*) fear reduction serves to increase the habit strength of any overt response with which it is contiguous; and (*c*) the implicit fear response has drive properties, then it can be deduced that under conditions of widely distributed practice, where inhibition due to work factors is largely obviated, a fear-motivated response will persist indefinitely with little diminution in strength.

This statement could also be made about a hunger-motivated response. But in the case of a primary appetitive drive like hunger, the presence of the motivational condition is insured on each trial, and reduction in strength of the hunger-motivated response, with nonreinforced trials, must be due to other factors. In the case of a learned fear drive, reduction in the strength of the fear-motivated response when shock is omitted may be mirroring some inhibition of the fear motive itself.

If the decrease in strength of fear-motivated responses in the absence of shock reinforcement, which has been reported, is due to some inhibitory work factor which has its origin in the overt response rather than in the implicit fear response, one might expect a considerable decrease in the strength of a fear-motivated skeletal muscular response under conditions of relatively massed practice, followed by strong recovery in strength with the passage of time, and little diminution in that response under widely distributed practice. The present experiment proposes to test these deductions.

METHOD

Subjects

Thirty-five female albino rats from the colony maintained by the Tulane psychology department were used. Twenty of these were naive rats, approximately four months old at the beginning of the experiment. The other 15 rats had previous experience in a problem-box apparatus, but had never been shocked or run in a runway. These rats were approximately five months old at the beginning of the experiment.

Apparatus

The apparatus duplicated one used by Amsel (1). It consisted of a white starting box with a grid floor 9 in. long, 2½ in. wide, and 3 in. high and a connected straight, white runway 72 in. long, 2½ in. wide, and 3 in. high, also with a grid floor. The runway opened into a black goal box 12 in. long, 6 in. wide, and 7 in. high, which had a wood floor. The bars of the grid in the starting box and runway were ⅛-in. brass rod, spaced ½ in. apart. The starting box and runway were covered with opal glass, and white paper was placed beneath the grids to eliminate irrelevant visual stimuli. A sliding guillotine door, painted white, separated the starting box from the runway. A swinging door located at the entrance to the goal box opened only from the runway into the goal box, and not in the reverse direction. It was painted white on the side toward the runway and black on the goal-box side. The goal box was covered with hardware cloth.

Alternate grid bars in the starting box and runway were wired in series so that when a rat touched alternate bars a circuit was completed. An electronic inductorium wired into the circuit provided a direct current that was broken five times a second by a relay. The relay made a fairly loud clicking sound. The current output was maintained at 220 microamps. The shock box had a large resistance incorporated so that variations in a rat's resistance had little effect on the amount of current received.

At points 4 in. from the starting box and goal box, 9-in. segments were cut out of the floor of the apparatus and hinged so that pressure on a segment would activate a microswitch. The distance between the two microswitches was 4 ft. These switches were connected to a timer in such a manner that pressure on the first switch started the clock and pressure on the second switch stopped it. In this way, a response measure of running time was obtained.

Eight small lights were spaced at equal intervals along the length of the starting box and runway, about 2 ft. above the apparatus. These lights could be controlled by *E* with a knife switch.

Procedure

Preliminary training. Food and water were in the living cages at all times. Following handling, each *S* was given six days of preliminary training. The purpose of this training was to minimize variability on the experimental days by allowing *S*s to explore the apparatus and learn how to go through the swinging door into the goal box. For the first three days of preliminary training the procedure was as follows: The *S*s were taken out of their cages, put into a large pen, left for 10 min., and removed one by one from there to the apparatus. Each *S* was placed first in the starting box, then in the runway, and finally in the goal box. From there, *S* was placed in a small cage, and then returned to the home cage. The doors in the apparatus were fastened so that S could not move from one section to another. On the first and third days, each *S* spent 5 min. in each of these four sections, and on the second day, *S* spent 10 min. in each of the four sections.

On the last three days of preliminary training, *S*s were taken out of the home cages, placed in the large pen, and left for 10 min. Each *S* was then placed in the starting box and left for 30 sec.; the door to the runway was opened, and *S* was allowed to run down the runway to the swinging door. The door was held partly open, and *S* was permitted to go through into the goal box, where it remained for 30 sec. The *S* was then put back into the runway, and the adaptation and training to the door were repeated. After this, *S* was placed in the small cage for 5 min. and then returned to the home cage.

The *S*s were run in a predetermined random order on each day throughout the experiment, regardless of experimental grouping.

Shock training. Following the last day of preliminary training, shock training began. Each animal was given one shock trial per day in a darkened room. On any one trial the following procedure was used: (*a*) *S* was placed in the starting box and 20 sec. were allowed to elapse; (*b*) *E* turned on the lights over the starting box and runway; (*c*) after the lights had been on for 2 sec., *E* activated the grid with shock and immediately raised the door of the starting box with a sharp snap; (*d*) *S* was continuously shocked until it entered the goal box; (*e*) as soon as *S* entered the goal box, the shock box (clicking sound) and overhead lights were turned off; (*f*) *S* remained in the goal box 1 min.; (*g*) *S* was placed in a small cage, where it remained for about 5 min., and was then returned to the home cage.

Experimental grouping. As each *S* reached its criterion of stable minimum running time over the 4-ft. segment, it was assigned to one of three experimental groups. The criterion was set at 7 out of 8 consecutive trials within five-thousandths of a minute variation in running time. The *S*s were assigned to the experimental groups so that the three groups were equated as closely as possible for mean number of trials to reach criterion, mean running time on all shock trials, and mean running time on the eight criterion trials. Any *S*s showing very atypical performance, such as very slow or very variable running speed, or failure to leave the starting box promptly or to enter the goal box promptly when being shocked, were eliminated in order to insure maximum comparability among the groups. Twenty-one of the original 35 rats were retained. The group differences in means for the three equating measures were slight and not statistically significant. Table 1 presents the data on matching of groups.

Procedure on test days. The procedure for any one trial on the test days duplicated the shock-training procedure in every respect, except that shock was never administered. The disconnected shock box was turned on, so that the sound of the switch and the clicking would produce, along with the onset of overhead illumination, a pattern of stimuli identical to those present during shock training. Each *S* in group I was given one trial a day for 60 days; each *S* in group II was given five trials a day for 12 days; and each *S* in group III was given 15 trials a day for four days, a total of 60 trials for each group.

TABLE 1

Mean Running Time under Shock and Mean Trials to Reach Criterion

GROUP	MEAN RUNNING TIME* (TOTAL TRIALS†)	MEAN RUNNING TIME (CRITERION TRIALS)	MEAN NO. TRIALS TO CRITERION
I	24.07	23.03	17.86
II	23.69	24.13	18.14
III	23.88	25.14	18.86
t (I and II)	.111	.404	.066
t (I and III)	.051	.272	.185
t (II and III)	.060	.699	.251

* Running time is reported in thousandths of a minute.

† The first two shock trials are not included in total trials because their extreme irregularity obscured the remainder of the data.

For *S*s in groups II and III there was a 2-min. interval between removal from the goal box on one trial and being put into the starting box for the next. They were placed in the small cage for 1 min. and then in the large pen for 1 min. They were taken from the large pen to the experimental apparatus. This procedure was followed to insure that the pattern of stimulation just prior to running in the apparatus was as comparable as possible for the three groups. The 2-min. interval was intended to insure that the stimulus traces from the preceding trial had dissipated (16).

RESULTS

Figure 1 presents mean running times for the three experimental groups over the 60 extinction trials. Inspection of the figure will show that the curve for group I (the one-trial-a-day group) is relatively smooth, and that it rises very little from the first to the last of the 60 trials. In contrast, the curves for group II (5 trials a day) and group III (15 trials a day) show considerable fluctuation from trial to trial, and there is a marked, though irregular, increase in median running time over the 60 trials. There is, however, a pattern to the irregularity; the sudden drops in the curves for groups II and III almost always occurred on the first trial of a day (trials 1, 6, 11, 16, etc. for group II, and trials 1, 16, 31, and 46 for group III). In groups II and III the peaks of the fluctuation are usually on the last trial of a day.

Because parametric tests of significance could not validly be made, the Mann-Whitney *U* test (9) was employed. Table 2 presents the results of this analysis for blocks of trials. The analysis was performed with both means and medians, where each mean or median is an average of an individual *S*'s performance over a block of trials. After the first 15 trials, the means of *S*s in group I were, in every case, significantly lower, at the .05 level of confidence, than those of group II. The difference between groups I and III was significant only over the last 30 trials. Analysis of the median data shows that in every case group I running time was lower than that of group II, but none of the differences reached signifi-

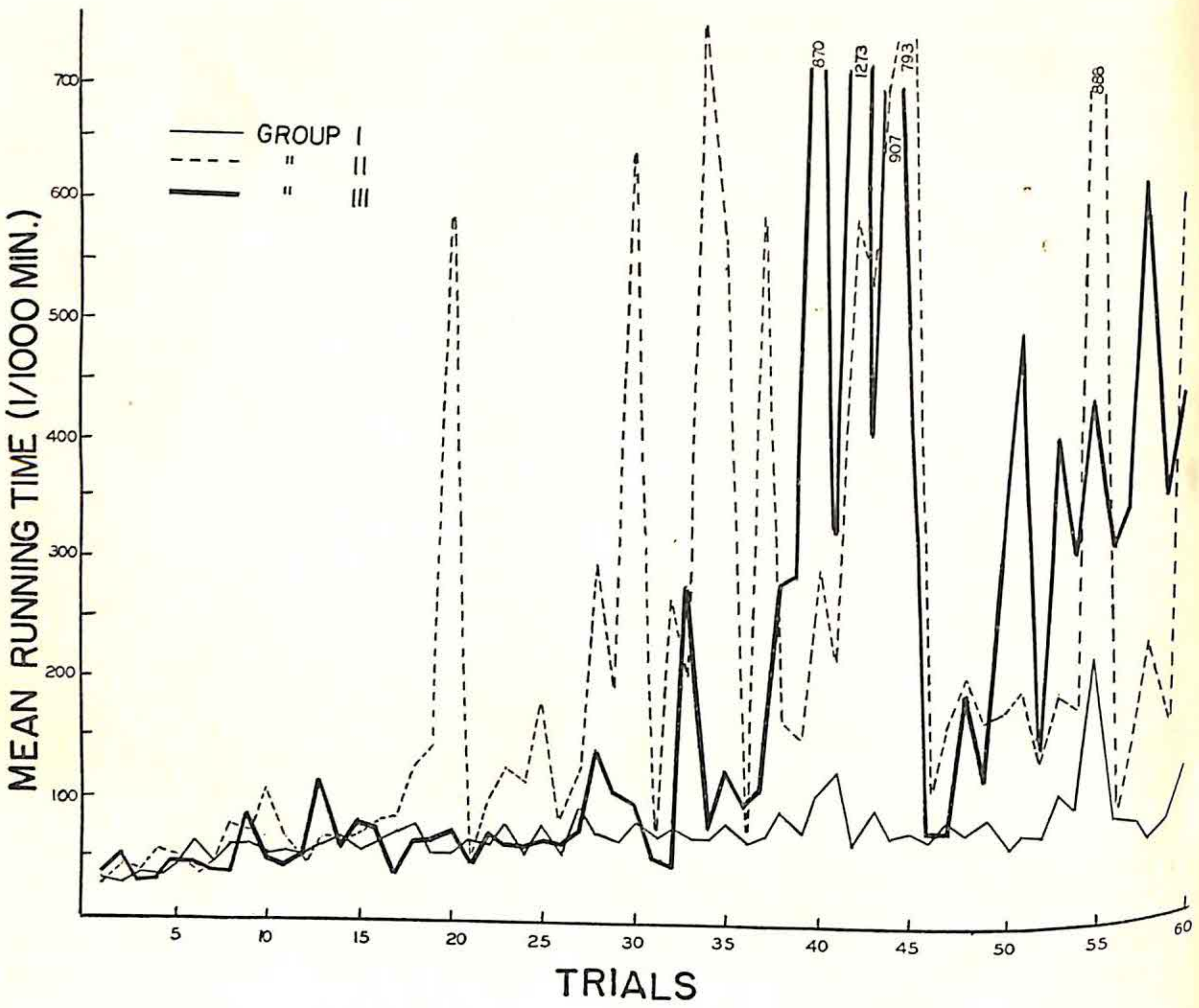

FIG. 1. Mean running time for three experimental groups on 60 extinction trials

cance. Group I medians differed significantly from group III medians only during trials 31 to 45. The mean data showed greater significance of differences because the means take into account the very long running times on the last trials of a day under massed conditions; in most cases these long running times did not affect the medians.

For both mean and median data, group III running time was significantly smaller than group II running time during trials 16 to 30; none of the other differences was significant.

In addition to the running time data, note was taken of other behavior of the rats during the extinction period. (*a*) The *S*s were rated on the speed with which they left the starting box (latency) after the door was raised. An *S* was rated "1 SB" if it left the starting box in less than 1 sec., "2 SB" if it left within 1 to 5 sec., "3 SB" if it left within 5 to 15 sec., and "4 SB" if the delay was over 15 sec. (*b*) Note was taken of whether *S* turned around in the starting box during the 20-sec. waiting period before the door was opened. (*c*) Each *S* was rated on how it entered the goal box after running to the end of the straightway: "1 GB" if it pushed the door open and entered by itself, "2 GB" if *E* had to hold the door open, and "3 GB" if *E* had to push the rat into the goal box. It was assumed that weakening of the fear-motivated response would manifest itself through an increased delay in leaving the starting box, in a lesser degree of orientation toward the door during the 20-sec. waiting period, and in refusal to enter the goal box readily. Observation in another experiment (1) indicated that failure to push through into the goal

TABLE 2

Probabilities Obtained by *U* Test on Mean and Median Running Times for Successive Blocks of Trials

GROUPS COMPARED		TRIALS				
		1–15	16–30	31–45*	46–60*	1–60*
I and II	Mean	.267 (I)†	.036 (I)	.007 (I)	.017 (I)	.002 (I)
	Mdn	.355 (I)	.159 (I)	.090 (I)	.090 (I)	.103 (I)
I and III	Mean	.500 (I)	.475 (III)	.017 (I)	.051 (I)	.026 (I)
	Mdn	.310 (III)	.191 (III)	.026 (I)	.267 (I)	.583 (I)
II and III	Mean	.310 (III)	.027 (III)	.500 (II)	.500 (II)	.402 (III)
	Mdn	.191 (III)	.013 (III)	.355 (II)	.500 (III)	.130 (III)

* *N* in group I = 6. For other groups, *N* = 7 throughout.
† Figures in parentheses indicate group with smaller running times.

box on reaching the end of the runway seemed related to weakening of the fear-motivated running response. No attempt was made to average the ratings, since they were not meant to represent equal intervals of any sort. However, for each group a mean was obtained of the number of trials on which the rats in that group exhibited each type of behavior. Table 3 presents the results of this analysis. In many cases the *N*'s involved are so small that the data are suggestive only.

The general picture presented by Table 3 is one which would lend confidence to a statement that group I differs from groups II and III in the direction of greater strength of fear-motivated responses. Twelve out of 16 of the differences between groups I and II and groups I and III are significant beyond the .05 level of confidence, and all 16 differences are in the expected direction. In only one case is a difference between groups II and III significant at this level, and these differences are not always in the same direction.

TABLE 3

Behavior in Leaving Starting Box and Entering Goal Box

CATEGORIES	MEAN NO. OF RESPONSES			*t* FOR EACH COMPARISON		
	Gr. I	Gr. II	Gr. III	I × II	I × III	II × III
1 SB	52.17	37.43	24.14	4.236*	5.210*	2.571†
2 SB	6.00	14.71	21.00	2.765†	3.958*	1.549
3 SB	1.67	4.86	11.00	2.573†	3.217†	2.241
4 SB	.17	3.00	3.86	1.826	3.181†	.486
Turning	13.67	28.86	21.00	2.086	.755	.783
1 GB	54.33	20.14	19.29	11.629*	5.458*	.142
2 GB	5.33	27.86	34.00	5.167*	4.119*	.859
3 GB	.33	12.00	6.71	2.339	2.703†	1.045

* Significant at .01 level.
† Significant at .05 level.

The running time data and those just presented are in general agreement: the differences between group I and groups II and III were marked and consistent, whereas no consistent and reliable differences could be shown between groups II and III.

DISCUSSION

The results of this experiment are in general conformity with the original hypothesis. That is, there was little diminution in strength of the fear-motivated running response when extinction trials were widely distributed, whereas in the massed conditions, extinction of the running response was more apparent. There was additional confirmation of the hypothesis in the observations made of other behavior. These indicated a greater manifestation of fear in the distributed-trials groups throughout the extinction series.

It has been suggested above that the more rapid extinction in the massed-trial groups might be due to work-inhibition factors. The various work or fatigue theories of extinction (4, 13, 17, 18) agree in general that the work involved in making a response, or the fatigue generated by responding, eventually act to reduce the strength of the response or to inhibit it entirely. They suggest that even under a continuous pain drive, there would be a gradual diminution in response strength as the number of trials increases. (Data presented by Amsel [1] show a gradual reduction in speed of running with successive massed trials under pain.) The work inhibition is conceived, in Hull's terms, as reducing the effective excitatory potential of the running response. It is possible that the work involved in the visceral and kinesthetic responses to the fear-arousing cues might result in some inhibition of the implicit fear response as well. In such a case we could speak unequivocally of the extinction of fear.

With distribution of trials, and the relatively slight amount of work inhibition built up by a single trial, elimination of the fear-motivated running response may be virtually impossible, unless there is some reduction in strength of the implicit fear itself. That some inhibition of the running response does occur even under widely distributed conditions is suggested by the slight rise in the curve for group I over 60 extinction trials. The present experiment cannot answer the question of whether this slight diminution in running speed is due to reduction in strength of the implicit fear or to conditioned inhibition based upon work inhibition present in making even a single response. A more adequate test would require a fear-motivated response that involved less effort than running a 6-ft. runway. However, the data of the present experiment do suggest that studies in which escape or avoidance responses are extinguished under relatively massed conditions are showing primarily extinction of the overt, fear-motivated response, rather than extinction of the implicit fear reaction.

There is some evidence that the rises in running time built up on each day in groups II and III do not depend upon, or result in, any permanent reduction in fear of the situation. This evidence is in Figure 1. It should be noted again that for group II the first trials of each day are trials 1, 6, 11, 16, 21, 26, 31, 36, 41, 46, 51, and 56; for group III the first trials are trials 1, 16, 31, and 46. Every trial is, of course, a first trial for group I. When the first-trial running times of group II are compared with the corresponding group I points, it can be noted that in only two cases—trials 41 and 51—is the group II point appreciably higher than the group I point. The first trial points of Group III are in all four cases practically identical with the corresponding points of group I. *U* tests performed on these data indicated that none of the differences was significant at the .01 level of confidence. Only two differences were significant at the .05 level. On trials 6 and 21, the points for group II were significantly lower than those for group I.

In other words, spontaneous recovery of the extinguished running response in the massed group brings its vigor of performance to practically the same level as that of the distributed group in almost every case where they are comparable. This means that the extreme loss in vigor of performance built up within any day in the massed-trial groups can be attributed more reasonably to peripheral work factors affecting the fear-motivated running response than to any permanent loss of fear. Whatever small *permanent* decrement in vigor is developed (presumably due to the build-up of $_{S}I_{R}$) apparently occurs in about equal amounts in the distributed and massed groups.

SUMMARY

An experiment was performed to test the effects of massing and distribution of extinction trials on the persistence of a fear-motivated instrumental response. The conditioned fear response was established by shocking the *S*s (rats) in a runway, and the response measure used was the time required to traverse the runway to a shock-free goal box. After being equated for their performance under the shock condition, three experimental groups received, respectively, 1, 5, and 15 extinction trials a day to a total of 60 trials. The results indicated that there was very little diminution in strength of the running response in the one-trial-a-day group, but a considerable diminution in strength of the response in the massed-trial groups on any one day. The one-trial group differed markedly from the other two groups; there were no important differences between the two massed groups. Recovery in strength of the running response after rest occurred in both massed extinction groups.

The discrepancy between the one-trial group and the massed groups was explained by work-inhibition factors which acted to inhibit temporarily the running response in

the massed-trial groups. It was suggested that the implicit conditioned fear response might persist indefinitely, and that data showing extinction of fear are, for the most part, showing primarily extinction of the overt fear-motivated response.

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Received June 17, 1953.

of the rats in the shock group one ECS per day for 10 days, or for 25 days in the second study. The procedure for administering the ECS was similar to that described by Braun, Russell, and Patton (2). A current of 20 Ma. applied for 1 sec. was sufficient to produce a severe grand mal convulsion. Immediately after a rat's convulsion had ceased, the animal was placed back in its living cage. Following the ECS series of the shock group and the corresponding rest period of the rest group, all the rats were given a 20-day retest, 10 trials per day, for the stability of their fixations.

RESULTS

In the 10-day study, 2 out of 15 rats in the shock group and 1 out of 14 in the nonshock group solved the discrimination problem in the postshock and postrest tests, respectively. In the 25-day study, 3 out of 12 rats in the shock group and 4 out of 13 in the nonshock group solved the discrimination. These differences, i.e., a difference of 1 between the shock and the nonshock groups in both studies, are obviously not reliable and indicate clearly that administration of a series of 10 or of 25 ECS under the conditions stated had no major effect on the stability of the rats' fixated responses.

Maier, Glaser, and Klee (9) have shown that the differences between the jumping response latencies to correct and incorrect stimuli can be used as an indication of the fact that the rat, although fixated, is nevertheless able to discriminate between the bright and dark windows. An analysis was made, therefore, of the response latencies of rats with position fixations that did not solve the discrimination

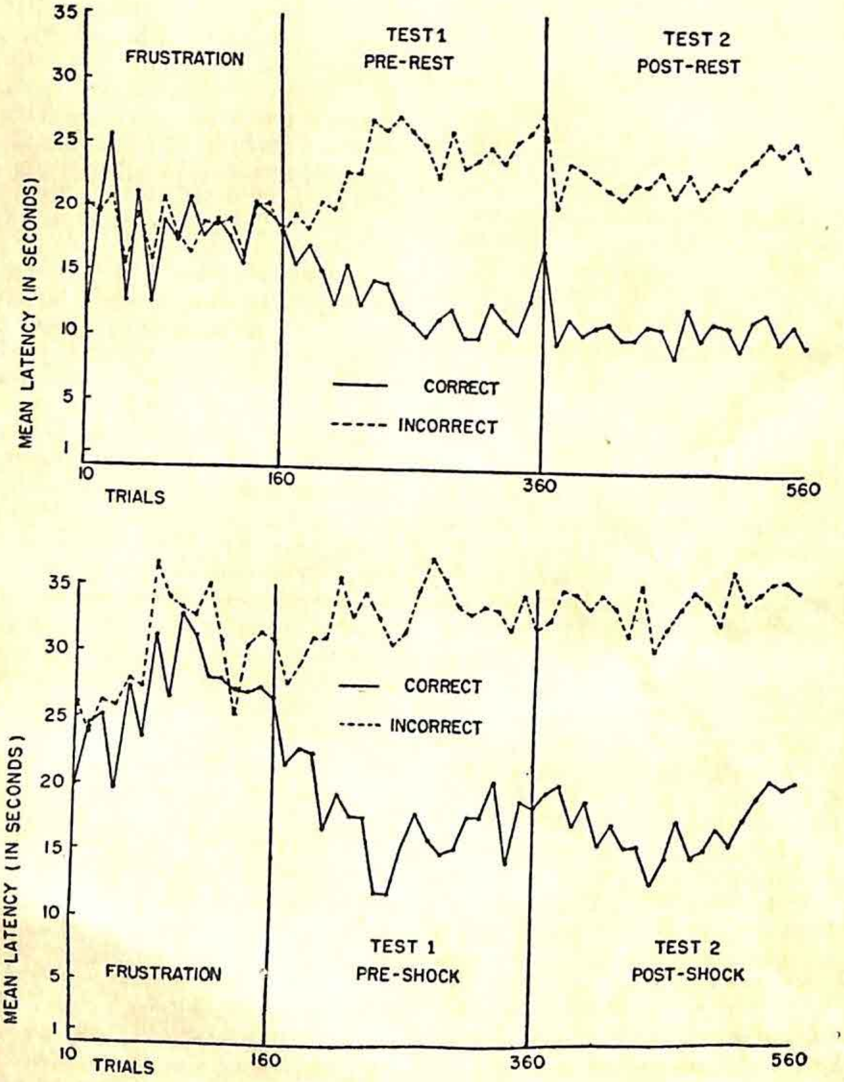

FIG. 1. Mean response latencies of rats with position fixations that did not solve the discrimination in the ten-day (ECS or rest) study

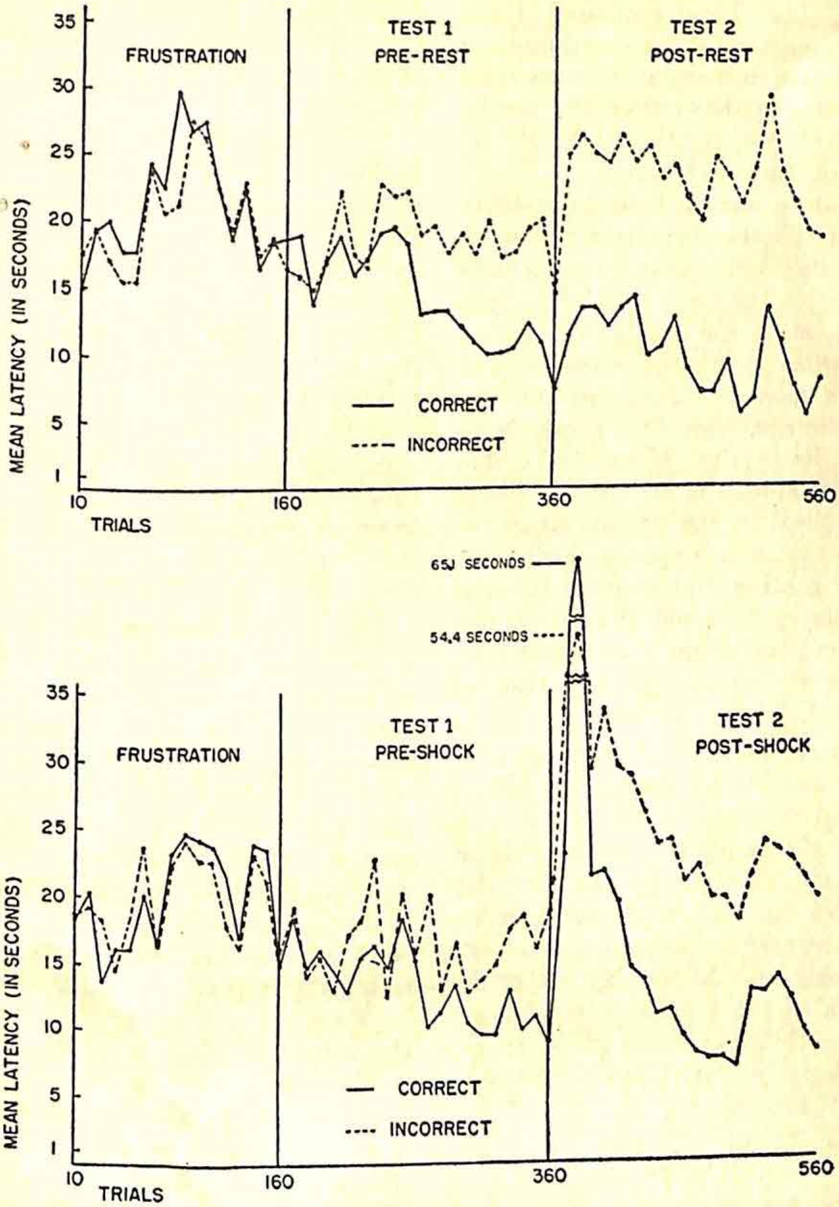

FIG. 2. Mean response latencies of rats with position fixations that did not solve the discrimination in the 25-day (ECS or rest) study

problem during the postshock or postrest fixation tests in the shock and rest groups of both studies. The results of this analysis are shown in Figures 1 and 2.

The latency curves of the 10-day study (Fig. 1) were plotted from the data of five animals in the shock group and six in the rest group. Those of the 20-day study (Fig. 2) were also plotted from five and six animals, respectively, in the shock and rest groups. A comparison of the curves of the upper and lower halves of Figure 1 shows that the difference in average latencies between the correct and incorrect responses of the shock and rest rats is about the same during the first and second tests for fixation. This indicates that a 10-day rest period, or the series of ten ECS applied to the shock group, did not result in any loss of the discrimination habit, at least as far as could be measured by comparing latencies.

However, a comparison of the upper and lower halves of Figure 2 shows that during the two days following the 25-day ECS series, the latencies of the correct and incorrect responses of the shock group increased. These increases may have been due to confusion on the part of the rats in making their discriminations, or they may have been the results of general retardation in their over-all responses following the shock series.

A further analysis was made of the stability of the fixated responses during the postshock and postrest tests for rats that failed to solve the discrimination problem. This analysis consisted of counting the number of times a rat deviated from its fixated response; i.e., if a rat had a fixated response to the left, any jump to the right would be considered a deviation from its fixation. It was found that no shock or rest animal in the 10-day group, and no rest animal in the 25-day group deviated from its fixated response during the second test for fixation. But seven of the nine rats in the 25-day shock group showed varying amounts of deviation from their fixated responses during the postshock test. Four of these altered their original fixations, three shifting from a response to the bright window to a position response, and the fourth shifting from a position response to the left side to a response to the right. Of the four, three had shifted their responses by the fifth day of the postshock test. Each of the three remaining rats showed a deviation from its original responses on only one day, either the first or second, of the postshock test. These results indicate that the series of 25 shocks caused some degree of variability in certain of the rats' fixated behavior.

CONCLUSION

From the above results it is concluded that the application of a 10- or a 25-day series of ECS under the conditions stated had no major effect on the stability of the rats' fixated responses, although the longer series of shocks produced minor degrees of retardation and/or confusion in the discrimination responses and minor degrees of variability in the fixated responses.

The question as to why the two ECS series did not have greater effect on the fixated behavior cannot be answered from the results. However, several possible reasons are as follows:

1. Fixated behavior established through frustration is especially resistant to alteration. This suggestion is supported by the work of Maier, Glaser, and Klee (9) and Maier and Klee (10).

2. The fixated response was overlearned during the 16-day frustration period and the 20-day preshock test period to the degree that the ECS had little or no effect. Experiments by Worchel and Gentry (14) and by Braun and Albee (1) lend support to this hypothesis.

3. The number of shocks administered each day was too small. The work of Worchel and Gentry (14) suggests this possibility.

4. Finally, the effects of the shocks were dissipated because of the time interval between shock and retest. The study by Duncan (3) bears on this point.

SUMMARY

Two studies were conducted to determine the effect of electroconvulsive shock (ECS) on fixated jumping behavior of the rat. The animals were trained, frustrated, and given a 20-day solvable problem discrimination test for the stability of their responses. Following this, they were divided into shock and rest groups. The shock animals in the first study were given a 10-day series of ECS, and those in the second study were given a 25-day series of ECS, while the rest animals of both studies rested the respective number of days. Following the shock, or the corresponding rest period, the rats were given a 20-day retest for the stability of their fixations.

The results showed that neither the 10-day series nor the 25-day series of ECS was effective in causing the rats to abandon their fixations and learn the solvable problem. However, they did indicate that the 25-day series of ECS caused an increase in the latencies of the jumping responses during the first two postshock days' trials in discriminating the positive from the negative stimuli. The 25-day shock series also caused some variability of the rats' fixated responses.

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Received June 24, 1953.

EFFECTS OF ANXIETY AND MORPHINE ON THE ANTICIPATION AND PERCEPTION OF PAINFUL RADIANT THERMAL STIMULI[1]

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Hill *et al.* (3, p. 473) have suggested that the emotional status of *S* may alter the results in pain perception experiments. Using electric shock as the stimulus, these authors demonstrated that when *E*'s attitude was reassuring, *S*'s pain threshold was approximately as high as it would have been had morphine been previously administered. Also, a combination of both reassurance and morphine was no more effective than either alone.

The present study is an extension of the experiment by Hill and his co-workers. It was undertaken to determine if similar results would be forthcoming when the more commonly employed thermal radiation technique was used and if a reduction of *S*'s anticipatory anxiety by a reassuring attitude on the part of *E* could be observed and measured by means of specific measures of anticipation. Thus, by extending Hill *et al.*'s findings, both in manner of stimulus administration and in method of measurement of *S*'s anticipation of the stimulus, it is possible to test the hypothesis that anticipatory anxiety is an important variable in pain perception experiments and that much of the analgesic action of previously administered morphine in such experiments is probably due to the diminution of this anxiety.

METHOD

Apparatus

Stimulator. The apparatus used to deliver the pain stimulus was similar to that developed by Hardy, Wolff, and Goodell (2). Heat from a 1,000-w. incandescent lamp was focused by a lens through a round aperture of 3.5 sq. cm. onto *S*'s forehead. The length of stimulation was determined by an electrically controlled timer that opened and closed a shutter which covered the aperture. This timer was preset for 3-sec. exposures.

Motor latency time. This measure was the time between the onset of the stimulus and the time *S* released a key held depressed with the left knee; the shorter the latency time, the greater was the anticipation. The *S* was instructed to release the key when he began to feel a burning sensation. At the onset of the stimulus a chronoscope was activated and then inactivated by the release of the key. Latency time was determined to the nearest hundredth of a second.

Galvanic skin response (GSR). The GSR apparatus consisted of a General Electric photoelectric-driven ink recorder, a General Radio (Model 715-A) direct current amplifier, a pentode tube, and a 45-v. B battery for supplying current to the pentode tube. This apparatus is a modification of one designed by Dr. R. C. Davis of Indiana University.

Three aspects of the GSR were studied. (*a*) "Anticipatory GSR's," defined as any responses that occur before the onset of the stimulus (the GSR apparatus was switched on from 3 to 9 sec. before the onset of each stimulus) and also as responses that appear up to 1.5 sec. after the onset of the stimulus. The assumption is made that any response appearing sooner than 1.5 sec. after the onset of the stimulus would be anticipatory. (*b*) "Latency of the GSR," defined as the time between the onset of the stimulus and the beginning of the GSR. This was determined in seconds. If no GSR appeared after the onset of the stimulus, the latency time for that particular response was scored as 3 sec. (*c*) "Amplitude of GSR"—the basal resistance before each response and the resistance at the maximum of the response were determined in ohms. These data were converted to changes in conductance (micromhos) (4), in order that GSR's obtained from *S*s differing in basal levels could be validly compared.

Subjects

Thirty-two postaddicts (individuals with previous histories of opiate addiction who had not received such drugs for several months prior to the experiment) were used as *S*s. They were randomly selected from *S*s available for research purposes at the United States Public Health Service Hospital, Lexington, Kentucky. All *S*s were serving sentences for unlawful possession of narcotic drugs.

Procedure

The *S*s were randomly placed in one of two groups. One group was called the "Formal" group, the other the "Informal" group. The *S*s in the Formal group were treated by *E* in a formal, impersonal manner, receiving neither reassurance nor explanation. The *S*s in the Informal group were treated by *E* in an informal, friendly manner, receiving reassurance and explanation designed to mitigate apprehension in the experimental situation. In general, *E* made an attempt to create an atmosphere of congeniality. The assumption was made that anxiety would be greater in the Formal than in the Informal group.

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[1] This paper is a portion of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of Kentucky, Lexington. A part of the experiment was presented at the 1952 meeting of the American Psychological Association.

The writer wishes to express his appreciation to Dr. James Calvin under whose direction this dissertation was completed, and to the members of the research staff of the U. S. Public Health Service Hospital, Lexington, Kentucky for their aid and helpful criticism throughout the course of this investigation.

[2] Now at the Biological Laboratory, Long Island Biological Association, Cold Spring Harbor, New York.

Each *S* was tested twice with an interval of one week between sessions. Half of each group was given 15 mg. of morphine injected subcutaneously during the first session, and the other half received the morphine during the second session.

Except for the difference in *E*'s formality, the procedure followed was similar for both groups. After a practice period *S*s received two "standard" stimuli of 370-w. intensity. Immediately after this, 15 mg. of morphine were injected subcutaneously, if scheduled. An hour later three series of nine stimuli were administered in a random order of intensities. Stimuli were spaced 90 sec. apart. The intensity of each series varied from 330 w. to 410 w. (216 to 280 millicalories/sec/sq cm). The *S*s were required to judge each stimulus as stronger or weaker than the previously delivered standards.

All data were combined into group means for the various measures. The significance of differences between groups was compared by means of the *t* test (1, p. 174) of significance.

RESULTS

The results for all data are summarized in Table 1. The comparison between control and morphine conditions when Formal procedures were used indicates that a statistically significant greater number of stimuli were called stronger under control conditions than under morphine conditions. Also, all the measures of anticipation, with the exception of amplitude of GSR, showed greater anticipation under control conditions than under morphine conditions at a statistically acceptable level of confidence. None of the comparisons between control and morphine conditions when Informal procedures were used yielded significant differences.

TABLE 1

Group Means, Differences between Means, and *t*'s for All Data

VARIABLE	GROUP	CONDITION		DIFF.	*t*	*p*
		Control	Morp.			
Number of stronger responses*	Formal	13.3	11.1	2.2	2.82	<.02
	Informal	12.1	11.1	1.0	1.00	>.30
Motor latency time (in sec.)	Formal	2.21	2.42	0.21	2.45	<.05
	Informal	2.44	2.57	0.13	1.46	>.10
Number of anticipatory GSR's†	Formal	18.81	12.25	6.56	2.74	<.02
	Informal	17.80	14.80	3.00	1.36	>.10
Latency of GSR (in sec.)	Formal	1.27	1.55	0.28	2.31	<.05
	Informal	1.55	1.79	0.24	1.69	>.10
Amplitude of GSR (in micromhos)	Formal	7.71	5.54	2.17	1.27	>.20
	Informal	5.36	4.68	0.68	0.75	>.40

* Maximum number of stronger responses is 27.
† Maximum number of anticipatory GSR's is 27.

Although more stimuli were called stronger and there was greater anticipation under Formal control conditions than under Informal control conditions, this difference did not reach an acceptable level of confidence.

DISCUSSION

The results are in general agreement with the findings of Hill and his co-workers. The verbal report and all the measures of anticipation with the exception of amplitude of GSR yielded significant differences between morphine and nonmorphine conditions when Formal procedures were used and failed to yield significant differences when Informal procedures were used.

There is, however, one point of apparent disparity between the present study and Hill *et al.*'s findings. The latter authors found that under Formal procedures *S*s overestimated the intensity of the test stimulus (standard stimulus), and when morphine was administered, the estimations were much more accurate; the mean was almost at the intensity of the test stimulus. This was not found in the present study except when the data for verbal report were broken down into an analysis of the number of stronger responses on the first series only. When this was done, it was found that *S*s did overestimate the test stimuli when Formal control procedures were used. One possible explanation of the discrepancies in the results is that the thermal radiation technique of stimulation is not as "threatening" to *S* as the electric shock used by Hill *et al.* A plausible explanation for the fact that overestimation was found only in the first-series data in this study might be that more anxiety would be expected when *S* was first brought into the experimental room than after he was accustomed to the situation. Hill and co-workers also found greater overestimation in the first three series of their experiment than in all six series (they used six series of nine stimuli each). An important difference in method of the two experiments is that when electric shock is used as a stimulus, *S* cannot escape from the expected painful situation, since the electrodes are securely fastened to his hand. In the present experiment, however, *S* merely had to withdraw his head and he escaped the painful stimulus.

The positive results obtained with verbal report strongly suggest that the conflicting results of earlier experiments employing the thermal radiation technique may be due to differences in the formality of the experimental procedures used; this could alter the amount of anxiety that *S*s might have in an experiment involving pain. The importance of *E*'s role is clearly demonstrated in this experiment. Differences in the interpersonal structure of the experiment result in discrepancies in evaluating the efficacy of morphine as a pain-relieving agent.

The failure of morphine to alter the measures of perception and anticipation of pain when anxiety is diminished suggests that morphine is only effective when anxiety is present and that much of the analgesic action of previously administered morphine in pain experiments is due to the diminution of the anxiety associated with the pain.

SUMMARY AND CONCLUSIONS

The effects of subcutaneous injections of 15 mg. of morphine on anticipation and perception of intensities of radiant thermal pain stimuli were studied under two conditions:

1. In Formal conditions *E* treated *S* in a formal, impersonal manner, giving neither reassurance nor explanation.

2. In Informal conditions *E* treated *S* in an informal, friendly manner, giving reassurance and explanation designed to mitigate apprehension in the experimental situation.

The assumption was made that anxiety would be greater under Formal conditions than under Informal conditions.

The *S*s were 32 postaddicts (individuals with previous histories of opiate addiction who had not received such drugs for a period of several months prior to the experiment). Along with the verbal report as to the intensity of the stimuli, motor and GSR measures of anticipation were recorded.

The following conclusions were drawn:

1. Morphine is most effective in raising the differential threshold to painful stimuli when anxiety is present.

2. When a procedure to mitigate anxiety is employed, morphine does not significantly raise the differential threshold to painful stimuli.

3. Morphine is effective in reducing the anticipatory responses to pain when anxiety is present.

4. When a procedure to allay anxiety is employed, morphine does not significantly reduce the anticipation of the painful stimulus.

5. There is some indication in this experiment that reduction of anxiety can be as effective as morphine in the relief of thermal pain and that morphine is only effective as an analgesic agent when anxiety is present.

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Received July 6, 1953.

APPROACH VERSUS AVOIDANCE IN AN AMBIGUOUS-CUE DISCRIMINATION PROBLEM IN CHIMPANZEES

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The purpose of the present study was to determine if there is any difference in the tendencies (*a*) to approach the positive stimulus and (*b*) to avoid the negative stimulus in a two-choice discrimination problem. Recently, Fitzwater (1) investigated the relative strength of these tendencies in rats by the method of "cue substitution." His results indicate that after a form discrimination has been firmly established rats approach the positive object with the same efficiency as they avoid the negative object. The present study differs from Fitzwater's in that an attempt was made to analyze approach and avoidance tendencies during rather than after the establishment of a discriminative response. An "ambiguous-cue" discrimination problem was employed which permitted separate presentation of "approach trials" (those providing only the positive stimulus) and "avoidance trials" (those providing only the negative stimulus).

METHOD

Subjects

Fourteen chimpanzees, their ages ranging from 5 to 29 years, were studied. Six *S*s (Bokar, Don, Dehn, Gamma, Helene, and Vera) were used for the three experimental problems, while the eight remaining *S*s (Ami, Alan, Coma, Dag, Ked, Nira, Pan, and Soda) were used for the preference test. All *S*s were considerably experienced with visual discrimination problems prior to the beginning of this study. The animals were housed in individual cages during the testing period and were given work sessions in the mornings before regular feeding.

Apparatus

The main part of the apparatus consisted of the testing tray shown in Figure 1. It was constructed entirely of 1-in. plywood. Two food wells, 1 in. deep and set 10 in. apart, were covered by identical square lids (4 in. on a side). At the leading edge of each food well were mounted two vertical supports acting as a frame into which 3-in. by 4-in. stimulus plaques could be inserted. The tray and the food covers were painted a flat gray. The tray was enclosed in a wooden superstructure which contained a vertically sliding, opaque screen.

Three pairs of stimulus plaques made of pressed wood were employed as test stimuli: plain black vs. plain white; horizontal black and white stripes vs. vertical black and white stripes (½-in. wide striations); and a black circle (radius of 1 in.) vs. a black triangle (2 in. on a side), both of which were painted on a white ground.

Procedure

The general training procedure for both the experimental problems and the preference test began with the screen in a lowered position. The *E* then adjusted the stimulus plaques and baited the proper food well. A trial was accomplished by raising the screen and slowly pushing the tray forward to a position where *S* reached through the wire mesh of its cage to displace one cover. If the choice was correct, *S* found a piece of fruit in the food well under the displaced cover. The tray was then drawn back, the screen lowered, and preparations were made for the next trial. The noncorrection method was used throughout.

Experimental problems. An ambiguous-cue discrimination problem was used to test the relative influence of approach and avoidance tendencies in chimpanzees. Three problems of this type were given to six *S*s to be learned to a criterion of mastery. The order in which the problems were presented was the same for all *S*s.

Problem I consisted of a black-white discrimination. Three *S*s were trained with white positive (the plaque to be approached) and black negative (the plaque to be avoided). The other three *S*s were trained with black positive, white negative. Only one stimulus plaque was present on any trial—either the positive or the negative plaque occupied one of the two frames, while the other frame remained empty. Thus, the positive plaque appearing below one cover (approach trial) signified the presence of food on that side. Contrariwise, the appearance of the negative plaque (avoidance trial) signified the absence of food on that side, consequently calling for a response to the other side—to the cover above the empty frame. Because the empty frame was as often rewarded as it was unrewarded, the cue to solution of the problem was the stimulus plaque. The order of presenting each of the two plaques followed a Gellermann series (2), while the position of each plaque varied from the right to the left frame in a prearranged irregular order. One session of 30 trials was given each day (15 approach trials and 15 avoidance trials) until a criterion of 16 consecutive correct responses was reached within a session.

Upon reaching the criterion of learning in Problem I, the animal was immediately assigned Problem II, involving the differentiation of horizontal striations–vertical striations. Three *S*s were trained with hori-

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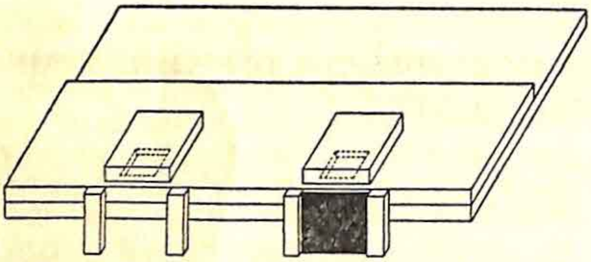

FIG. 1. Diagram of the test tray showing a black stimulus plaque set in one of the two frames

TABLE 1

Error Scores Made on Approach Trials and Avoidance Trials for Each of the Three Experimental Problems

TRIALS	RANGE	MEAN	p*
Problem I			
Approach	27–117	67.3	<.05
Avoidance	61–140	90.2	
Problem II			
Approach	38–74	56.3	<.02
Avoidance	62–90	77.2	
Problem III			
Approach	20–102	76.0	>.05
Avoidance	78–136	99.2	

* Calculated by Wilcoxon's method for paired replicates (7).

zontal stripes positive, vertical stripes negative, while the other three *S*s were trained with vertical stripes positive, horizontal stripes negative. The procedure was the same as that followed in Problem I, save that training was terminated when *S* made 12 successive errorless responses within a session of 30 trials.

After mastering Problem II, *S* was given training on Problem III, which required the discrimination of circle-triangle, the circle being positive for three *S*s. The main difference between Problem III and Problems I and II was the presence of a "neutral" yellow plaque on each trial. That is, the relevant cue along with a plain yellow plaque appeared on every trial; the yellow plaque was placed in the frame opposite to that occupied by the positive or negative plaque. Training was continued until *S* made 12 consecutive correct responses within a session of 30 trials. Use of the yellow plaque on each trial served as a control for a possible preference by the animals to approach a plaque rather than an empty frame. This preference may have arisen from previous experience with problems which required the animal to displace stimulus plaques in order to obtain food.

Preference test. As a further test of possible preference for a stimulus plaque over an empty frame, eight new chimpanzees were required to master a plaque vs. empty-frame discrimination. Four animals (Plaque Group) were trained to choose the cover over a plaque and to avoid the cover over an empty frame. The remaining four animals (Empty-Frame Group) had to choose the cover over an empty frame and to avoid the cover over a plaque. A white plaque was used for two *S*s in each group and a black plaque for the other two *S*s in each group. The plaque was presented in random order in the left and the right frames, and training was terminated when *S* made ten successive errorless responses. A preference for displacing the cover over a plaque rather than a cover over an empty frame would be indicated by better learning scores for the Plaque Group.

RESULTS

The six *S*s that were trained on Problems I, II, and III required a mean of 363.3, 306.7, and 403.2 trials, respectively, to reach the criterion of mastery. Table 1 presents the error data for each problem in terms of those made on approach trials and those made on avoidance trials.[2] In Problem I the difference between the mean error scores of the approach trials (67.3) and the avoidance trials (90.2) is significant at the .05 level of confidence. That is, the *S*s performed more efficiently on trials in which the positive cue was present than on trials in which the negative cue was present. In Problem II approach trials were again significantly easier to master than avoidance trials. The data for Problem III are not as extreme as those obtained from the two previous problems; although the difference between the mean error scores is large and in the same direction, this difference lacks statistical significance.

Performance on Problem III, which involved the use of a neutral yellow plaque on each trial, suggests that the animals did not prefer the cover to a stimulus plaque in Problems I and II. This is borne out by the results of the preference test, where one group of four *S*s (Plaque Group) learned to approach the stimulus plaque, while the other group of four *S*s (Empty-Frame Group) learned to avoid the stimulus plaque. The Plaque Group required a mean of 22.3 trials and 9.3 errors, whereas a mean of 22.0 trials and 10.8 errors were required by the Empty-Frame Group;

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[2] Individual data for Problems I, II, and III and for the preference test are contained in tables which can be obtained by ordering Document 4155 from American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, ℅ Library of Congress, Washington 25, D. C., remitting in advance $1.25 for microfilm or $1.25 for photocopies. Make checks payable to Chief, Photoduplication Service, Library of Congress.

neither difference approached statistical significance. (For individual data, see footnote 2.) It would seem, therefore, that the greater efficiency of performance on approach trials obtained in all three experimental problems cannot be attributed to preferential tendencies operating at the beginning of discrimination training.

DISCUSSION

The results of each of the three ambiguous-cue discrimination problems showed that fewer errors were made on trials which furnished the positive plaque as against trials which furnished the negative plaque. These data are interpreted as indicating that chimpanzees learn an approach habit more readily than they learn an avoidance habit. That is, the animals learned to approach the positive plaque (100 per cent reward) which was present on "approach trials" with greater efficiency than they learned to avoid the negative plaque (0 per cent reward) which was present on "avoidance trials." It will be noted that the empty frame—or yellow plaque—was rewarded on half the trials and consequently did not provide a differential cue upon which a response could be based. This approach-avoidance description may also take the form of a "conditional reaction" (3). In Problem I, for example, the *S*s may have learned to approach the plaque when it is black and to avoid it when it is white. This is essentially the same interpretation as that already proposed and leads to the same conclusion that an approach habit is established more efficiently than an avoidance habit.

Description of the chimpanzee's performance in terms of response selection (6), however, leads to difficulty. If the animals learned left- and right-going responses to specific configurations of stimuli, approach trials and avoidance trials should have been mastered with equal facility. Since approach trials were significantly easier to master, and since recent evidence (4, 5) places doubt upon the concept of response selection, performance on the experimental problems seems more appropriately described on the basis of approach-avoidance to specific stimulus plaques.

In explaining the differential approach-avoidance effect, reinforcement theorists may take the position that reward of the correct response (which leads to approach behavior) contributes more to the learning of a discrimination problem than nonreward of the incorrect response (which leads to avoidance or nonapproach behavior). Perceptual theorists, on the other hand, may contend that the positive object represents a more effective cue for a discriminative response than the negative object. The adequacy of the two theoretical possibilities will depend upon future research.

SUMMARY

This experiment was designed to determine if there is any difference between the tendencies to approach the positive object and to avoid the negative object in an ambiguous-cue discrimination problem. Six chimpanzees were required to learn each of three separate discrimination problems in which response to one of two identical food covers was determined by the presence of the positive cue on some trials and by the presence of the negative cue on other trials. In all three problems, fewer errors were made on trials providing only the positive cue as against trials providing only the negative cue. Control measures revealed that preferential tendencies were not operating to produce this difference. These results were interpreted in terms of differential mastery of approach and avoidance habits.

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Received May 8, 1953.

GENERALIZATION OF AN AVOIDANCE RESPONSE TO VARYING INTENSITIES OF SOUND

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The phenomenon of stimulus generalization, as well as a suggestion of the form of generalization gradients, was apparent in some of the classical conditioning experiments of Pavlov (10). Since that time, other studies have more thoroughly investigated stimulus generalization utilizing classical conditioning techniques (e.g., 1, 2, 5, 6). The relatively few investigations that have been concerned with this phenomenon in instrumental-response situations have for the most part employed approach responses (e.g., 3, 4, 9, 11). Further knowledge about the occurrence of generalization and the variety of situations in which it is manifested would be obtained if an avoidance training situation were used. Interest in avoidance conditioning accrues from its tendency to result in a greater resistance to extinction than approach training. Hence, resistance to extinction of an avoidance response may be sufficiently sensitive to reflect the effects of changes in the dimension of the conditioned stimulus.

None of the studies measuring an instrumental response has made use of sound intensity for the dimension of the conditioned stimulus with which to test the presence of stimulus generalization. Recent interest in intensity per se and its possible effect on gradients of generalization (8) makes it seem desirable to investigate responses given to varying degrees of sound intensity and then to evaluate those responses not only as a function of the extent of deviations from the original conditioned stimulus value, but also in terms of the direction of the deviations.

The present study is an attempt to discover some of the effects of sound intensity on gradients of generalization utilizing a shock-avoidance technique. Animals were conditioned to make an avoidance response following a buzzer of a certain intensity, and then generalization was tested by extinguishing separate groups at differing intensities

METHOD

Subjects

The *S*s were 30 naive female albino rats obtained from the colony maintained by the zoology department at the University of Denver. The weight range was from 55 to 159 gm., with an average of 103.7. The *S*s were assigned at random to six groups of five rats each.

Apparatus

The apparatus consisted of a straight runway 50 in. long and 5 in. wide with a goal box at each end measuring 7 by 12 in. The apparatus was not covered but measured 28 in. in depth so that none of the *S*s could escape. The rods of the grid floor were spaced ¼ in. apart, as measured from the inner circumference, to allow feces to drop through. The grid was electrified by the use of an inductorium operated with a single dry cell of 1.5 v. The secondary coil of the inductorium was set so as to deliver a current of 2 v. as measured across the grid. Since the rats were being conditioned to sound, an ordinary commercial buzzer was placed at the side of each end box. The buzzers were mounted on Celotex and then placed on cotton in order to keep vibration at a minimum. The buzzers were connected to a variable transformer and the current regulated so as to obtain three intensities of loudness. These intensities, which are referred to as low, middle, and high, operated from voltages of 38, 72, and 138, respectively. Approximations of relative differences in decibels were obtained with a Vu meter, and an estimate of the absolute intensity of the lowest sound was made by using a masking sound produced by a Maico E2 audiometer. The microphone was placed 20 in. from the buzzer. This procedure resulted in decibel readings of 93, 99, and 108 for low, middle, and high intensities, respectively. Accurate timing of buzzer-shock relationship was obtained by placing masonite discs on the shaft of a kymograph cut in such a way that the part left protruding would strike and depress a switch for the desired length of time. The kymograph, revolving at a rate of 1.745 rpm, would present the following sequence: (*a*) buzzer at left end box, duration 0.04 min., entire grid free from shock, (*b*) buzzer off, shock in left end box and runway, (*c*) shock off, buzzer at right end box, duration 0.04 min., (*d*) buzzer off, shock in right end box and runway. The kymograph was placed in a different room from that of the apparatus so that extraneous learning cues from the running of the motor and clicks of the switches might be eliminated from the learning situation. A mercury switch operating the kymograph was placed in the experimental room, and *E* could interrupt the kymograph sequence as desired.

A fluorescent light illuminated all parts of the apparatus equally.

Conditioning Procedure

No preliminary handling or orientation was utilized. All *S*s were kept in home cages near the experimental room for one week prior to the experimental session. Food and water were available at all times. The conditioning procedure began by placing *S* in one of the end boxes. Both end boxes were used as starting boxes in a counterbalanced order for *S*s within each group. The *S* was forced to stay in the starting box because shock was present in both the runway and the goal box. After *S*'s initial exploratory behavior had subsided (2 min. or more), *E* started the kymograph, which caused the buzzer at the side of the starting box to sound. During operation of the buzzer, 0.04 min., the entire apparatus was free from shock. Immediately after cessation of buzzer, shock came on in starting box and runway, forcing *S* to run to the goal box to escape punishment. On the next trial, this end box then became the starting box. Time between trials was varied by stopping the kymograph for differing intervals. A trial was considered successful when *S* ran from the starting box to the goal box while the buzzer was sounding, thereby avoiding all shock. The *S*s were run to a criterion of five consecutive trials in which shock had been avoided. If *S* failed to learn after 125 trials, it was discarded. Only three *S*s had to be replaced because of failure to reach this criterion. After *S* reached criterion, the buzzer was adjusted to the appropriate loudness, shock turned off, and extinction trials started immediately. Each *S* was conditioned and extinguished in one experimental session. The criterion of extinction was failure to leave the starting box during each of five successive soundings of the buzzer.

Groups and Conditions

One half the *S*s were conditioned to an intensity of 108 db. This group was then divided at random into three groups of 5 *S*s each; one group extinguished to a buzzer of 108 db, one to 99 db, and one to 93 db. The remaining 15 *S*s were conditioned to an intensity of 93 db, divided into three groups, and extinguished as above. The strength of the generalized responses was computed by comparing the number of trials to extinction of the various groups.

RESULTS

Two measures were taken: the number of trials to reach criterion during the avoidance conditioning, and the number of trials to reach the criterion of extinction. The former measure is of significance in demonstrating that the three extinction subgroups within each avoidance training condition did not differ significantly in the number of trials to acquire the avoidance response. Also, it is of some importance to ascertain whether those animals conditioned to the high intensity of buzzer differed significantly from those conditioned to the low intensity in number of conditioning trials. The data on the number of learning trials for each group are presented in Table 1.

TABLE 1

Mean Number of Learning and Extinction Trials for Each Group

STIMULUS INTENSITY DURING CONDITIONING (db)	STIMULUS INTENSITY DURING EXTINCTION (db)	TRIALS TO CRITERION OF LEARNING		TRIALS TO CRITERION OF EXTINCTION	
		Mean	*SD*	Mean	*SD*
108	108	54.8	35.7	53.0	64.2
	99	49.0	23.1	43.4	31.1
	93	51.8	14.4	6.4	1.2
93	108	64.8	27.3	33.2	14.2
	99	79.0	38.0	29.2	34.0
	93	81.0	35.9	34.4	31.1

Bartlett's test of homogeneity of variance for the subgroups conditioned to the high intensity of buzzer yielded a chi square of 3.62, which for 2 *df* falls considerably short of the .05 level of confidence. A simple analysis of variance between these three subgroups resulted in an *F* less than unity. A comparable analysis was made of the three subgroups conditioned to the low buzzer. Bartlett's test resulted in a chi square of 2.20. The *F* was again less than unity. A *t* run between the two avoidance training conditions was 1.92, which for 28 *df* falls short of the .05 level of confidence.

The number of trials to reach the criterion of extinction for each of the subgroups is presented in Table 1. Although it was intended to utilize the analysis of variance technique on the extinction measures, Bartlett's test of homogeneity of variance resulted in a chi square of 37.11, which for 5 *df* is highly significant. Consequently, Wilcoxon's *T* (13) for unpaired replicates was used in comparing these data. Since direction as well as magnitude of differences was the concern of this study, it was necessary, in order to use the one-tailed test, to extend the probability table by using the formula derived by Wilcoxon (12).

In comparing the groups that were conditioned to the high intensity of buzzer, 108 db, the following results were found: (*a*) the difference between groups extinguished at

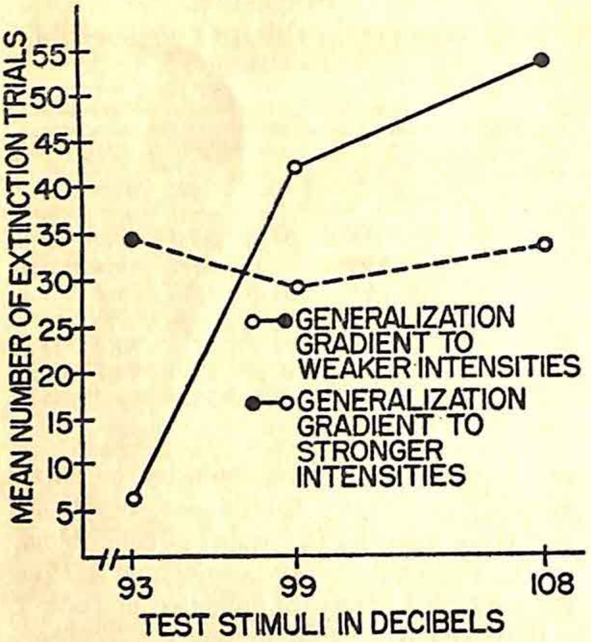

FIG. 1. Gradients of generalization as a function of deviations from originally conditioned stimulus values

108 db and 99 db was not statistically significant; (*b*) the difference between groups extinguished at 108 db and 93 db was significant at the .05 level; (*c*) the difference between groups extinguished at 99 db and 93 db yielded a *p* of .005. The resulting generalization gradient is plotted in Figure 1.

In comparing the groups conditioned to low intensity of buzzer, 93 db, it can be seen in Figure 1 that the mean extinction trials obtained at the various extinguishing intensities closely approach a horizontal line. As one might expect, no significant differences were found between any of the three groups.

DISCUSSION

It has been demonstrated that generalization occurs to varying intensities of sound in a shock-avoidance situation. The results are generally in agreement with those reported by Brown (3) and Hovland (6). The generalization gradient shown in Figure 1 indicates a relatively steep gradient for animals conditioned at 108 db and extinguished at lesser values, whereas the gradient plotted for animals conditioned at 93 db and extinguished at louder intensities closely approaches a horizontal line. It should be noted that the failure to find a significant difference between animals extinguished at 108 db and those extinguished at 99 db in the former gradient may be in part due to the fact that a subjective scale of loudness differences is unknown for the white rat, resulting in an arbitrary selection of these stimulus intensities. It seems apparent, therefore, that stimulus intensity does have some influence on the form of a generalization gradient, and that the tendency to respond as measured in this experiment may be a joint function of two things: (*a*) the difference between the training and test stimuli, and (*b*) the intensity of the test stimuli.

Any conclusion concerning the exact slopes of the two gradients is tenuous in view of the extreme variability of the data as well as the fact that only three test points were selected along the stimulus dimension. However, an inspection of the medians for the various extinction subgroups yielded gradients similar to those plotted for means.

It is interesting to note that the difference between the number of learning trials for the high and low conditioned groups closely approached significance at the .05 level, with the groups conditioned to low intensity taking the greater number of trials to learn. Even though there is comparatively little knowledge concerning generalization as a function of the number of reinforcements, the available evidence (7, 10) indicates that relative extinction rate of generalized responses should be more rapid the further the process of conditioning has advanced. If this statement is applicable to the present study, it seems unlikely that the two different gradients obtained can be explained on the basis of differing number of conditioning trials since the groups having the greater number of reinforcements required approximately the same number of trials to extinguish the generalized responses as the original conditioned response. This consideration appears to place even more importance on the effect of intensity per se on generalization.

SUMMARY

1. Thirty female albino rats were trained to make an avoidance response following the sounding of a buzzer. Fifteen *S*s were conditioned to a sound intensity of 93 db and 15 to an intensity of 108 db. The response was extinguished at three different levels of loudness to determine the magnitude of generali-

zation. Five *S*s from each avoidance training condition were extinguished at 108 db, five at 99 db, and five at 93 db.

2. Two generalization gradients were plotted in terms of the mean number of trials required to reach the criterion of extinction: one gradient for *S*s extinguished at greater intensities, and one for *S*s extinguished at lesser intensities. A much steeper gradient of generalization was found when moving from high to low intensities than when moving from low to high.

3. It was demonstrated that stimulus intensity as used in this shock-avoidance situation had an influence on the form of the generalization gradient. It would appear that the tendency to respond may be a joint function of the difference between the training and test stimuli and the intensity of the test stimuli.

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Received May 27, 1953.

THE EFFECTS OF INTERFERENCE ON RESPONSE STRENGTH[1]

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It is rather commonly believed (though without much systematic evidence) that interference in its various forms leads to some kind of distinctive or generalized "emotional" state, often termed *frustration*, which in turn energizes behavior. Available data do indicate that interruption situations are often followed by increased vigor of response (2, 4, 7, 8). A relationship between response strength and interference is also suggested by such nonexperimental observations as the increases in voice intensity, "aggressiveness," foot stamping, etc., which frequently follow everyday interference situations.

This article reports evidence concerning the effects of interference in a delay situation on response strength as measured by the rate of turning a crank. Several facets of interference were investigated. Interference was introduced at two distances from a subgoal; the interference situation was repeated on successive trials to determine possible cumulative effects; and two work levels were imposed in view of the possibility that work (fatigue) may be positively related to the energizing effects of interference (1).

METHOD

Subjects

A total of 40 children of both sexes, between 45 and 70 months old, were used as *S*s. Twenty-five of the *S*s were attending the University Elementary School; 15 *S*s were attending kindergarten at the public elementary school at Coralville, Iowa. All *S*s scored 100 or better on Stanford-Binet tests. Most of the *S*s were accustomed to participating in "games" with experimenters or testers.

Apparatus

The apparatus consisted of a large box on the face of which was a crank, a vertical panel of 12 jeweled lights, a marble dispenser, and a red light. Turning the crank operated a sensitive relay which activated the succeeding events. If desired, the apparatus could be manually controlled from an adjacent room from which *S* could be observed. A counter relay lit each panel light, one at a time, proceeding from the top of the panel downward. At the bottom light, a solenoid dispensed a marble into a small cup. The apparatus could be set either (*a*) to provide an uninterrupted succession of the panel lights at regular 5-sec. intervals to final pay-off of marble at the bottom light, or (*b*) to stop at any point in this sequence for a period of 30 sec., returning to the topmost panel position during the final 5 sec.; the onset of this delay period was signaled by a buzzer, and its duration was accompanied by a red light. This second setting constituted the interference situation used in the present investigation.

The panel-light sequence mechanism operated independently of the speed at which *S* turned the crank. However, if *S* stopped turning the crank, the progression of lights was reversed. Each half-revolution of the crank was recorded on a polygraph, together with the succession of panel lights, the number and duration of crank stops by *S*, and the onset and duration of the interference situation. Rate of crank turning was computed by counting the number of "pips" over the desired interval and dividing by two.

Experimental Design

Rate of crank turning was studied as a function of three experimental variables: (*a*) interference, (*b*) position of interference (nearness to marble subgoal), and (*c*) work. Two levels of each variable were administered.

There were four independent groups of 10 *S*s each, assigned at random to 2 × 2 combinations of interference and work. Each *S* received both positions of interference. For later reference, the 2 × 2 interference and work groups may be arranged as follows:

HI	HN
LI	LN

where H and L stand for the higher and lower work conditions, and I and N stand for the interference and noninterference conditions. Two positions of interference were administered to each *S* on each interference trial so that comparisons of the effects of this variable involved the *same* *S*s.

Procedure

Two sessions were administered to each *S* individually on separate days. Session I (preliminary) introduced *S* to the procedure and rules of the situation and provided data on rate of turning under noninterference conditions for all 40 *S*s. On each of 11 trials, lights proceeded normally down panel at 5-sec. intervals to the twelfth position, at which a marble was dispensed.

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[1] This paper is based in part upon a dissertation submitted in partial fulfillment of the requirements for the Ph.D. at the State University of Iowa. The author wishes to express his thanks to Dr. Vincent Nowlis.

[2] Now at the University of Mississippi.

It took 55 sec. for completion of this panel sequence. The *S*s learned to wait for the sound of a bell before beginning each trial. This between-trials rest interval was 30 sec. for all trials. The *E* turned the crank part of the time during the first trial in order to demonstrate the method. No record was made of this trial, but *S* received a green marble to place on the marble board. The rate of turning was recorded for the following 10 trials. Each *S* received a total of 11 marbles. For Session I only, *S* filled a 7-hole marble board and received 4 useless marbles (red marbles) on the other four trials. (These four nonrewarded trials were in a random sequence and were found effective in maintaining interest during the preliminary training period.) During all but the first (unrecorded) trial, *E* was out of the room.

Session II (experimental) followed after not more than seven days. The general procedure was the same as in Session I. Different marble boards were used, and the marble board was filled twice, *S* receiving a take-home prize each time.

As described earlier, the interference condition (groups HI and LI) was a 30-sec. delay and return of the panel light to the beginning position. On each interference trial, two such delays were introduced successively, once at the fourth panel light and once at the eleventh panel light (order randomized). Following these two delays, the lights proceeded downward normally to the twelfth light, where a marble was received and placed on the marble board. Each interference trial, then, included two delayed and one nondelayed panel sequence, followed by receipt of a marble. The first trial of Session II was a nondelayed sequence involving the normal 55 sec. This was followed by four interference trials as described, a marble being received at the end of each. Marbles were placed in a five-hole marble board. At the end of these five trials, *S* turned in the marbles for a take-home prize. For trials 6 to 10 this procedure was repeated, trial 6 being a nondelayed trial. Thus, during Session II there were eight interference and two noninterference trials. The usual 30-sec. between-trials interval was given following receipt of each marble.

The main difference between the interference and noninterference conditions was whether delay occurred before or after receipt of a marble. The 30-sec. delays were introduced at the same positions for both interference and noninterference groups. Interference *S*s, however, received no marble during delay periods, while noninterference *S*s received a marble at the beginning of each delay, making it in effect a between-trials interval for noninterference *S*s. Thus, noninterference *S*s received eight extra marbles, since HI and LI *S*s had four interference trials or eight delays while filling their marble board. To make the time taken to fill the marble board the same for interference and noninterference *S*s, noninterference *S*s were given a 13-hole (rather than a 5-hole) marble board. Though the variable of marble-board size is thus confounded with the interference variable, this is considered less important than introducing a difference in time required to fill the marble board.

The higher- and lower-work groups differed in terms of whether or not *S*s were required to turn the crank during the 30-sec. delay periods. Since two 30-sec. delays were presented on each interference trial, the higher-work *S*s turned the crank 1 min. longer per interference trial than the lower-work *S*s. Each delay period was timed by a clock which operated automatically with the onset of interference. For HI and HN *S*s, this clock ran only while *S*s turned the crank during delay periods. For LI and LN *S*s, the clock ran only when *S*s were *not* turning the crank during delay periods.

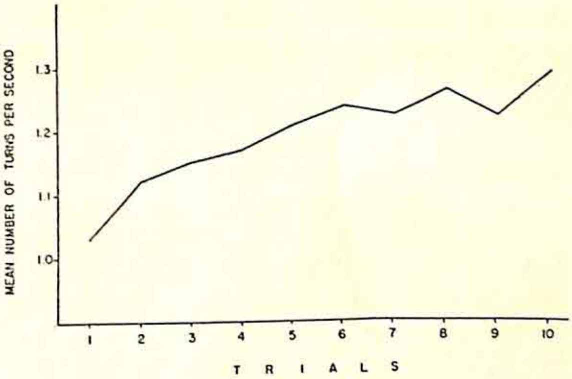

FIG. 1. Mean rate of turning per trial for the four groups during Sessions I and II

RESULTS

Session I

Figure 1 shows the mean rate of crank turning per trial for Session I based on the total sample of 40 *S*s. During Session I, mean rate per trial gradually increased from 1.03 turns per second at the first trial to 1.31 turns per second at the tenth trial, an increase of .28 turns per second. This difference is significant at the .001 level of confidence ($t = 7.44$, $df = 39$).

There were marked differences among the 40 *S*s in mean rate on trial 1 of Session I. The possibility was investigated that the slope of the rate × trials curve might be affected by the initial (trial 1) rate. The 10 highest and 10 lowest *S*s in trial 1 rate were selected and the rate × trials rate plotted. The curve for initially high *S*s was comparatively flat; the curve for initially low *S*s increased steadily toward the level of the other *S*s. An analysis of trends (6, pp. 350–351) was applied to these curves and the trials × rate interaction variance proved significant beyond the .01 level of confidence ($F = 26.13$, $df = 9$ and 162). This suggests the possibility that increasing rate may reflect increasing motivation from different initial levels owing to irrelevant drive components introduced by receiving marbles, filling holes, etc., in a manner similar to that assumed by Hull (5, pp. 253–254) for dominant and nondominant drives.

Session II

Initial analysis was made in terms of mean rate differences between trials $1 + 2$ and trials $9 + 10$. The mean rate per trial for each S was the mean rate for *all* panel positions and all panel sequences within each trial. On interference trials, the means include two delayed and one nondelayed sequence.

Mean changes in rate for HI and HN Ss were $+.204$ and $-.109$ turns per second, respectively; those for LI and LN Ss were $+.061$ and $+.085$. Positive signs refer to increases in mean rate, negative signs to decreases. When data were arranged in a 2 × 2 table, the interference × work interaction variance was not significant ($F = 2.95$, $df = 1$ and 36, $p < .10$).

In the analysis of the simple effects, the above data, which involved only the first two and last two trials, were not used. A more conservative analysis of the simple effects was thought advisable in view of the nonsignificant interference × work interaction variance. Further analysis is in terms of differences in trend between the various simple effects in which relative changes in rate for each of the 10 trials is taken into account. These tests involved the hypothesis that the differences between the population means of the groups were the same for each trial; the pooled trials × Ss interaction variance of the respective groups served as the error term.

The trend comparisons for the different groups are shown graphically in Figure 2. The means of the different pairs of groups have

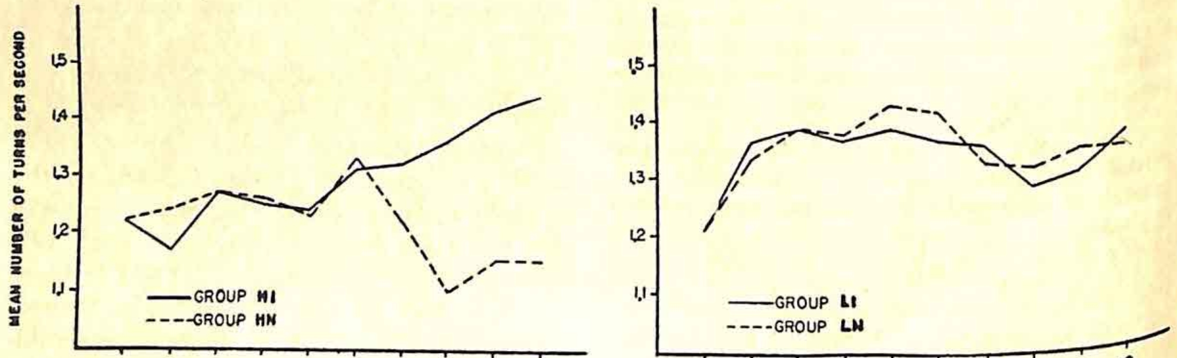

FIG. 2. Comparison of the different pairs of groups in terms of relative changes in rate per trial during Session II. (A constant correction was applied to the means of the dashed group of each pair.)

been equated for initial rate. A difference in trend significant beyond the .001 level ($F = 4.25$, $df = 9$ and 162) was obtained for the comparisons between the HI and HN groups (Fig. 2*A*). None of the other trend comparisons proved to be statistically significant.

Rate of crank turning during interference. Since LI and LN *S*s were instructed to stop turning the crank during the 30-sec. delay periods, data involving rate during interference are available only for *S*s assigned to the higher-work conditions. Statistical analysis involved the mean rate for 30-sec. periods obtained on each trial following the fourth and the eleventh panel positions separately. An analysis of differences in trend was applied to the delay-position × trials rates for the separate HI and HN groups. Since both the fourth and eleventh light positions were administered to the same *S*s, a three-dimensional analysis was made testing the hypothesis that the differences between the delay-position true means were the same for all interference trials. This analysis yielded no significant trend differences between the fourth and eleventh light rates for either the HI or HN groups. On the other hand, when delay-position was disregarded, the analysis of trend differences between HI and HN groups during interference yielded a group × trials interaction variance significant beyond the .001 level ($F = 4.31$, $df = 7$ and 126). The trial-by-trial rate for these groups during interference followed a pattern similar to that shown in Figure 2*A* for the over-all rate change with trials.

Additional observations. Both interference groups showed similar verbal and behavioral changes during interference trials, such as swearing, shouting, or hitting apparatus, an increasing intensity (loudness) of verbal responses, and so forth. Such behavior was completely absent in both noninterference groups.

DISCUSSION

In general, these results substantiate the proposition that an interference situation under the conditions defining higher work has an energizing effect on rate of crank turning and that this effect is some positive function of the number of successive presentations. Different interpretations are possible, namely that the energizing effect was the result of the lower frequency of marble reinforcement or the smaller marble-board size associated with the interference condition (see *Procedure*). However, in view of other experimental material involving the effects of periodic reinforcement (e.g., Skinner's [8] observations of the negative relation between time between reinforcements and rate of bar pressing), it seems reasonable to regard the possible effects of the differences in frequency of marble reinforcement as favoring HN rather than HI *S*s. The fact that no differences appeared between HI and HN *S*s during the first five trials (Fig. 2*A*), when both groups completed their respective marble boards, suggests the unimportance of the smaller marble board used by HI *S*s.

Significant trend differences were obtained only for the higher-work comparisons. The importance of the work variable here is inconclusive due to the indirect method by which work differences were defined. The variable of higher work was confounded with the variable of turning or not turning the crank during the interference delay periods. Turning or not turning may have introduced effects in addition to those of rest or fatigue. Qualitative observations of the behavior of LI *S*s were indicative of disturbed or "aggressive" behavior similar to that exhibited by HI *S*s and suggest that the lack of lower-work differences in rate may be an artifact of the defining operation for lower work. Within the present design it is impossible to estimate the contribution of such effects, and conclusions concerning the importance of the work variable must await the use of other methods of varying work level.

The panel position or nearness to marble subgoal at which interference was introduced had no significant differential effect on rate. This is not surprising since the energizing effects of interference were cumulative rather than localized within the panel sequence. The comparison of the higher-work interference and noninterference groups during successive delay periods indicated the same effects on rate obtained during the nondelayed parts of the panel sequence.

SUMMARY

The present article has reported the effects of an interference situation on ongoing response strength, measured by rate of crank turning, under two levels of work and at two distances from marble subgoal.

Forty preschool children, 45 to 70 months old, were used as *S*s. Each *S* learned to turn a crank continuously while a light moved downward through 12 panel positions. On reaching the final panel position, a marble was dispensed into a cup. The marbles were used to fill holes in a wooden block which, when completed, entitled *S* to a reward. There were two sessions, given on separate days. Session I provided data concerning changes in rate as a function of trials (marbles) under noninterference conditions. Session II included two interference (30-sec. delays) and two work conditions and a within-groups comparison involving interference at two separate panel positions. All *S*s received marbles and, ultimately, take-home rewards. Eight interference and two noninterference trials were presented during Session II.

The major results of the investigation were as follows:

1. Session I mean rate increased significantly with successive trials.

2. There was a significant relationship between initial rate and later change in rate with trials on Session I: the higher the initial rate, the less the later change in rate.

3. For *S*s under the higher-work condition, mean rate of interference *S*s increased with trials throughout Session II; mean rate declined for noninterference *S*s during the last half of Session II.

4. The panel position at which interference was introduced had no significant differential effect on rate.

5. Both interference groups (higher and lower work) exhibited "aggressive" and disturbed behavior, during Session II, which seemed to increase in intensity with successive trials. No such behavior was exhibited by noninterference *S*s.

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Received July 13, 1953.

DELAYED-PUNISHMENT EFFECTS MEDIATED BY COMPETING BEHAVIOR

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It has been demonstrated in previously reported experiments (2, 3) that behavior can be strengthened, maintained, and controlled in a relatively precise fashion simply by manipulating the time interval by which a response delays the occurrence of a brief shock. While all behavior emitted by the organism in this situation may be paired with the noxious stimulus, the avoidance response is unique in that its occurrence always puts off the shock (1). This provides a greater average interval between the avoidance response and shock than is the case for any other recurrent response. As a consequence, the avoidance response comes to dominate all other forms of behavior with respect to frequency of occurrence. The present experiment was designed to permit direct measurement of changes in the rate of occurrence of a sample of this other behavior.

METHOD

Apparatus, Subjects, and General Procedure

The general shock and control apparatus have been described in (3). The *S*s were six male rats, laboratory-bred descendants of the Wistar strain, ranging in age from 110 to 125 days at the start of experimentation. Experimental sessions, each 2 hr. long, occurred five days each week, the animals running at the same time every day, two animals at a time. Between sessions, the rats were housed in individual cages, with water and Purina Laboratory Chow pellets continuously available. No food or water was ever present in the experimental boxes.

Two bars were available to the animals, each protruding through an H slot in adjacent walls of the experimental box. Each bar was hooked up to a timing relay, which controlled the time of onset of shock. Duration of the shock, controlled by another timer, was fixed at 0.2 sec. Depression of either bar accomplished two things: it disconnected the timer controlled by the other bar from the shock circuit, and it reset its own timer, thus delaying the appearance of the shock for a preset interval of time. This interval remained constant on one bar (C bar) throughout the experiment. On the other bar (V bar), the interval was varied according to the design outlined below. Occurrence of the shock disconnected both these timers from the shock circuit and put a third one into operation. This third timer controlled the interval between shocks as long as no bar depression occurred.

The procedure is illustrated in Figure 1. In this sample record, the first three shocks occurred without any bar presses, and were under control of timer 3, set at 10 sec. Four seconds after the third shock, a response was made on bar C. This put timer 1 into operation, the next shock coming 20 sec. after the response. The duration of the bar press had no effect upon the delay interval, which was controlled only by the initial downward press on the bar. Six seconds after the fourth shock a response was made on bar V. This put timer 2 into operation, and the next shock came 40 sec. after that response. The remaining section of the record can be read the same way, with each occurrence of a given response putting its own timer into operation and shutting off the other timers.

Experimental Design

Response rates were obtained for each animal at various combinations of delay intervals on the two bars. Each animal was run on a given combination of intervals until a steady total rate was maintained, i.e., until the rate of responding on both bars combined changed by no more than 0.1 responses per minute in any two out of three consecutive sessions. Only the second hour of each 2-hr. experimental period was used in computing these rates, for reasons already presented (3). When the total rate met this criterion of steadiness, the delay interval on bar V was changed. This procedure was repeated for a range of intervals, keeping the delay on bar C constant at all times.

Response rates presented below are those prevailing during each criterion period. For animals 8 and 11, the interval on bar C was 15 sec., and for animals 6, 7, 12, and 92, it was 20 sec., as indicated by the arrows in Figure 2. The interval between shocks, if no response occurred, was 10 sec. for animals 6, 8, and 12, and 5 sec. for animals 7, 11, and 92. These differences could not be correlated with any systematic variations in the data.

Curves relating the delay interval on the V bar to the rate of responding on each of the individual bars

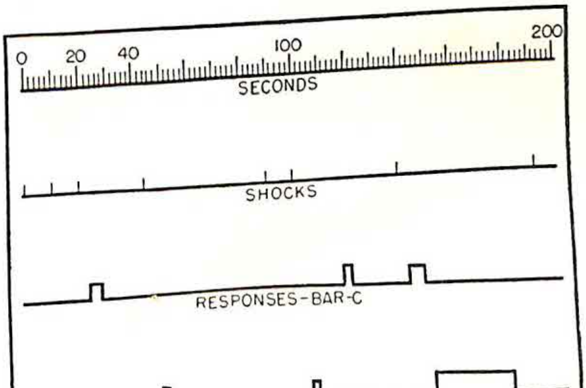

FIG. 1. The experimental procedure (see text for detailed explanation)

were secured from each animal. The points on each of the curves were ordered in a different sequence, with the exception that the first point obtained in each case was the one at which the delay interval on the two bars was equal.

RESULTS

Log response rates as a function of the log delay interval on the V bar are presented for each animal in Figure 2. As the delay interval decreases, the total response rate on both bars increases in a roughly linear fashion up to a maximum, on the other side of which there is a slight decline. The curves for the individual bars are considerably more irregular than the total curves, but this is to be expected since the criterion for recording a datum point was in terms of the steadiness of the total, rather than the individual, rates. The major features of the V- and C-bar curves, however, are consistent from animal to animal.

The V rate, like the total, decreases from a maximum as the delay of the punishment increases. At the left of the maximum, however, the rate decreases sharply. The rate on the C bar shows a steady decrease with the increasing delay interval on the V bar. These functions characteristically intersect at an interval close to that which was maintained on the C bar. On either side of the point of intersection the curves diverge rapidly, the higher rate prevailing on the bar which delays the shock for a longer period of time.

When the delays on the two bars approach equality, the effect of uncontrolled variables acting to determine a "preference" becomes apparent. This is indicated by the fact that the intersection of the curves is displaced from the point at which the two bars produced equally delayed shocks (indicated by the arrows in Fig. 2).

DISCUSSION

Examination of Figure 1 shows that the delay interval on the C bar, though maintained at a constant timer setting, is not independent of the interval on the V bar. A V-bar response occurring shortly after one on the C bar effectively increases the average delay interval on the latter bar, although the minimum delay is still 20 sec. For this reason, the decline in rate of responding on the C bar with increasing delay intervals on the V bar is not unexpected. Results obtained previously in a single-bar situation have demonstrated this inverse relation between rate and delay interval (3).

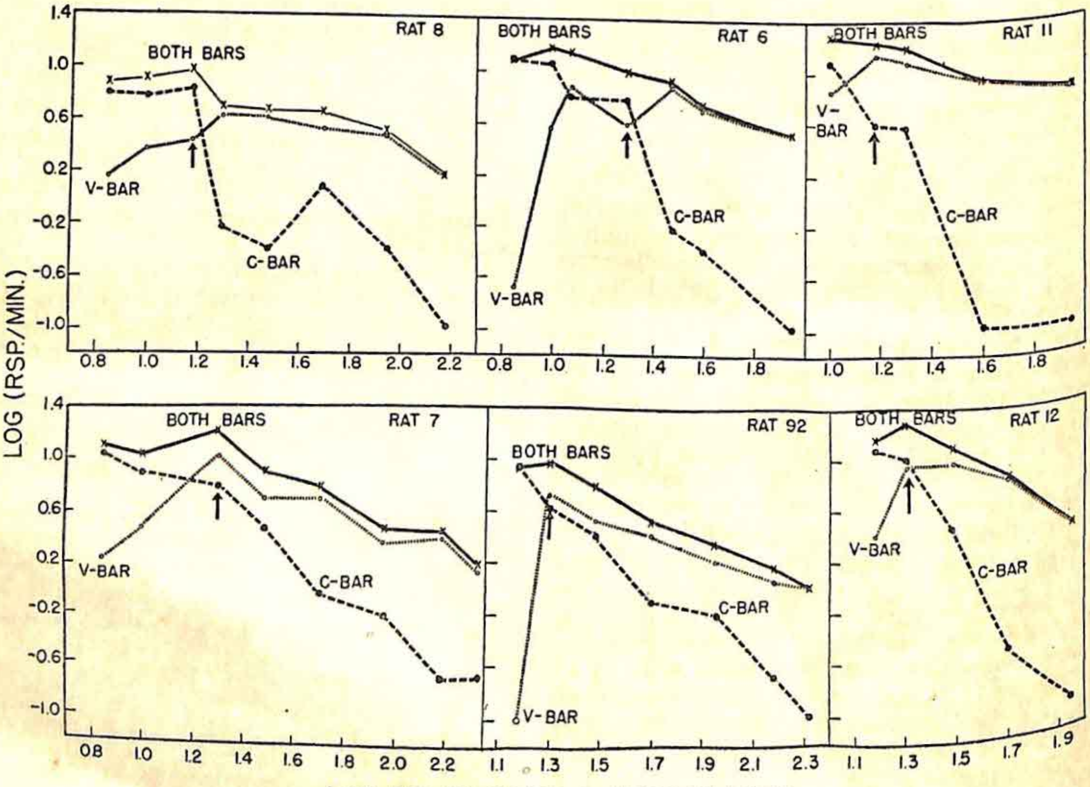

FIG. 2. Total rate of bar pressing and the rate on each individual bar plotted as a function of the shock-delay interval on the V bar. Arrows indicate the points at which both bars produced equal delays.

This decrease in rate with longer shock-delay intervals can be attributed to a lowered probability that any given nonavoidance behavior will be paired more closely in time with the shock than will the bar-pressing responses. Thus, the number of different behaviors which can successfully compete with bar pressing is increased, and the avoidance rate goes down. The more rapid decrease in rate on the C bar is a reflection of the C bar's relative disadvantage in meeting this competition, because of its lower minimal delay.

A comparison of the V-bar curves with those obtained in a previous experiment (3) further emphasizes the necessity for considering competing behavior in any evaluation of the effects of delayed punishment of a given response. Conditions in both experiments were similar except that only one bar was used in the earlier one. The relevant comparisons are with those curves obtained with 5- or 10-sec. shock-shock intervals (interval between shocks if no bar press occurs), since those are the values used here. In the former case, the maximum in the curves occurred at approximately 5 or 10 sec., depending upon the shock-shock interval used. In this experiment, the maximum in the V-bar curves occurs at approximately 15 or 20 sec., depending upon the delay interval on the C bar.

A relatively long delayed punishment, then, will decrease the probability of a response if some other behavior, punished after a slightly longer delay, is available. If no such alternative response is available, behavior will be maintained even in the face of relatively quick punishment.

As the shock delay produced by the V bar becomes less than that produced by the C-bar response, the avoidance rate comes to be maintained almost exclusively on the C bar. Compared with the gradual decline of the C-bar rate at the right of the intersection of the two curves, the V bar declines very rapidly at the left of this point. This indicates that a small difference between two responses, with respect to the time by which they delay punishment, has a much greater effect in altering relative response probabilities at short than at long delay intervals.

SUMMARY

Six white rats learned avoidance responses under the following procedure. Brief electric shocks of fixed duration were delivered every few seconds unless the animal pressed either of two available bars. Depression of either bar delayed the shock for a specified interval. This interval remained constant on one bar (C bar) throughout the experiment but was varied through a range of values for the other bar (V bar). Curves were secured from each animal relating the delay interval on the V bar to the total rate of responding, and to the rate on each of the individual bars. The following observations were noted:

1. On a log-log plot, both the total rate and the rate on the V bar decrease linearly from a maximum as the delay of punishment increases.
2. At short delays, the rate on the V bar decreases rapidly almost to zero, while the total rate is maintained solely by the C bar.
3. The rate on the C bar shows a steady decrease with the increasing delay interval on the V bar.
4. The curves for the two responses intersect at a point somewhat displaced from the interval at which they produced equally delayed shocks. On either side of this point the curves diverge rapidly, the higher rate prevailing on the bar which delays the shock for a longer time.

In addition to confirming results previously obtained in a slightly different situation, the data warrant the following inferences:

1. The effectiveness of delayed punishment in depressing behavior depends upon the availability of other responses which produce a less immediate punishment.
2. Small differences between responses, with respect to the delay of punishment, have a much greater effect in altering relative response probabilities at short than at long delay intervals.

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Received June 1, 1953.

THE DIURNAL ACTIVITY PATTERNS OF CAGED MIGRATORY WHITE-CROWNED SPARROWS IN LATE WINTER AND SPRING[1]

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For more than a century it has been known that caged migratory birds, particularly nocturnal migrants, frequently develop a marked restlessness during the migratory season. According to von Homeyer (23) a description of this phenomenon in the nightingale (*Luscinia megarhyncha*) was recorded as early as 1822 by Naumann. In Finland and Germany, where this nocturnal unrest has been investigated quite extensively, it has been known usually as *Zugunruhe*. Empirical descriptions of *Zugunruhe* have been published for several species by Wagner (24), Palmgren (15), Promptov (17), and others. The literature on "natural" and experimentally induced *Zugunruhe* has been reviewed by Palmgren (15, 16), van Oordt (22), Farner (7), and Steinbacher (20).

Most of the attention in research has been directed toward the *Zugunruhe* of thrushes (Turdidae) and old-world warblers (Sylviidae). In spring it has been observed generally that the period of *Zugunruhe* begins about the same time as spring migration and tends to last considerably longer than the natural migratory period, frequently until the beginning of postnuptial molt. The *Zugunruhe* of these species is manifested most characteristically by a period of pronounced activity between evening and midnight; however, some individuals may show a period of relatively intense activity shortly before dawn, whereas others may be almost continually active throughout the night. In general these species show little nocturnal activity during nonmigratory periods. To the best of our knowledge, no pattern resembling that of the *Zugunruhe* of nocturnal migrants has been reported for nonmigratory species.

Although the available information on *Zugunruhe* is highly interesting and suggestively analogous to actual migratory behavior, it is for the most part based on relatively small samples of behavior of small numbers of *S*s under unnatural conditions. However, we agree with Palmgren (16) in the opinion that the investigation of *Zugunruhe*, if applied very cautiously in comparison with diurnal activity patterns for nonmigratory periods, may be useful in studying certain aspects of the psychology and physiology of migration.

Little attention has been given to the activity patterns of caged fringillid finches during the migratory season.[3] These species are of considerable interest since many of them migrate, at least in part, during the day. Palmgren (14) in a very limited number of observations on the greenfinch (*Chloris chloris*) and the chaffinch (*Fringilla coelebs*) found no evidence of well-developed nocturnal activity. Also, Bergman (3) indicates no evidence of typical nocturnal *Zugunruhe* in his limited observations on the activity and depth of sleep of several fringillid species. Promptov (17), however, has reported the development of a definite nocturnal *Zugunruhe* in young scarlet grosbeaks (*Carpodacus erythrinus*) in fall. Eyster (6) has found that a vernal nocturnal unrest develops in caged slate-colored juncos (*Junco hyemalis*) and white-throated sparrows (*Zonotrichia albicollis*); both are migratory species. In the migratory white-crowned sparrow (*Zonotrichia leucophrys leucophrys*) Eyster observed nocturnal activity throughout the year in captivity; however, maxima were observed in spring and fall. It is of further interest to note that the nonmigratory ploceid finch, the English sparrow (*Passer domesticus*), showed no nocturnal activity whatsoever.

As one aspect of our investigation of physio-

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[1] This investigation was supported by funds provided for medical and biological research by the State of Washington Initiative Measure No. 171.

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[3] The recent paper by Eyster (*Ecological Monographs*, 1954, **24**, 1–28) appeared after this manuscript went to press.

logic cycles of a migratory race of a fringillid finch, the white-crowned sparrow (*Zonotrichia leucophrys gambelii*), we have made extensive recordings of the diurnal activity patterns of caged individuals during late winter and spring. It is the purpose of this paper to describe these activity patterns with respect to the normal development of the vernal *Zugunruhe* and to present correlations of the development of *Zugunruhe* with certain physiologic and environmental changes.

METHOD

The white-crowned sparrows (*Zonotrichia leucophrys gambelii*) used in these experiments were captured with Japanese mist nets from the population which winters in the canyon of the Snake River of southeastern Washington. A separate series of recently captured birds was used each year. The randomly selected birds were permitted to become conditioned to the cages and diet before the investigations were begun. On autopsy, all experimental birds were found to be males. Both in 1952 and 1953 the experiments were begun in early March and continued until May 24. Table 1 summarizes the number of birds used and the number of bird days (24-hr. days) recorded.

The birds were maintained in an outdoor aviary on the campus of the State College of Washington, where they were relatively free from extraneous noises and lights. The system employed for recording activity patterns has been described in detail in an earlier publication (8). Briefly, an electric signal marker registered on a continuously moving paper tape each time the centrally located spring-suspended perch assembly was depressed by the weight of the single bird in an activity cage (9 by 14 by 11 in.). The caged control birds, as well as the activity cages containing the birds for recording, were kept in large (8 by 12 by 6 ft.) cages covered with hardware cloth. These large cages were provided with partial overhead and lateral shelter to reduce exposure to precipitation and wind.

Throughout the period of captivity, including the recording periods, the birds were provided with water, grit, and food ad libitum. The food consisted of red millet seed, supplemented in 1952 with Pablum (Mead, Johnson, and Co., Evansville, Indiana) and chopped fresh vegetables; in 1953, the red millet seed was supplemented with a vitamin- and mineral-enriched poultry mash prepared by the Department of Poultry Science, State College of Washington.

Observations on plumage were recorded each week at the time of weighing. Wild birds and caged controls from the same population were collected and autopsied periodically to obtain data on lipid deposition, testicular development, and molt. At the conclusion of the period of activity-recording, the birds whose activity had been recorded were autopsied; they were found to be similar to the wild and caged controls with respect to the degree of testicular development and lipid deposition.

At autopsy the gonads were placed in alcohol-formaldehyde-acetic acid fixing mixture for several days to allow thorough impregnation; then, the two testes from each male were weighed rapidly on a Roller-Smith Precision Balance. Carcasses were frozen for subsequent extraction of lipids. The data obtained from these ether extractions are expressed as a ***lipid index***, i.e., the number of grams of ether-extractable lipid obtained from the carcass per 100 gm. body weight immediately after death. The observations on plumage included arbitrary designations of the intensity of molt as follows: no molt = 0, light molt = 1, medium molt = 2, and heavy molt = 3. Although somewhat subjective, these designations were found to be useful when used constantly by one investigator with a fixed set of criteria. The molt of the caged birds was similar in pattern and sequence to the natural prenuptial molt of wild birds during the same period.

Weekly mean temperatures were obtained from the records of the meteorological station at the State College of Washington. The natural photoperiod, as used here, is the time between sunrise and sunset plus civil twilight in both morning and evening.

RESULTS

The temporal distribution of activity among the individual birds was found to be remarkably similar; however, there were some substantial variations in the quantity of recorded activity. In part this was doubtless the result of individual differences in the daily quantity of activity. However, we are also convinced that the habits of the individual birds with respect to striking the perch and, indeed, the differences in sensitivities of the different perch-microswitch assemblies were also important contributing factors. Therefore, in calculating the composite activity patterns (Fig. 1 and 2) for the four to six birds recorded

TABLE 1

Schedule of Recording

PERIOD	1952		1953	
	NUMBER OF BIRDS	BIRD DAYS RE-CORDED	NUMBER OF BIRDS	BIRD DAYS RE-CORDED
Mar. 8–14	4	26	5	35
Mar. 15–21			5	35
Mar. 22–28	4	27	5	35
Mar. 29–Apr. 4			5	35
Apr. 5–11	4	27	6	42
Apr. 12–18			6	42
Apr. 19–25	4	28	6	42
Apr. 26–May 2			6	42
May 3–9	4	28	6	42
May 10–16			6	42
May 17–23	4	28	6	42

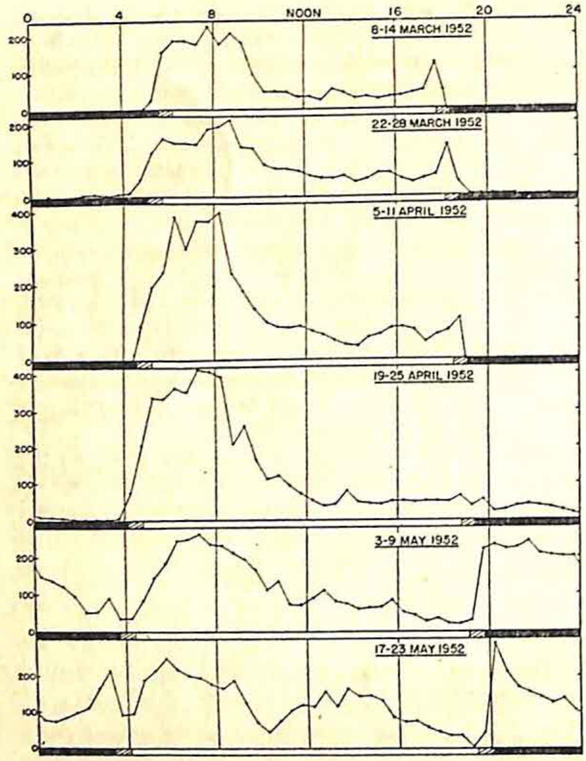

FIG. 1. Composite diurnal activity patterns of caged male *Zonotrichia leucophrys gambelii* for late winter and spring of 1952. Black bars designate the period of darkness; diagonally hatched bars, civil twilight; and open bars, the period between sunrise and sunset.

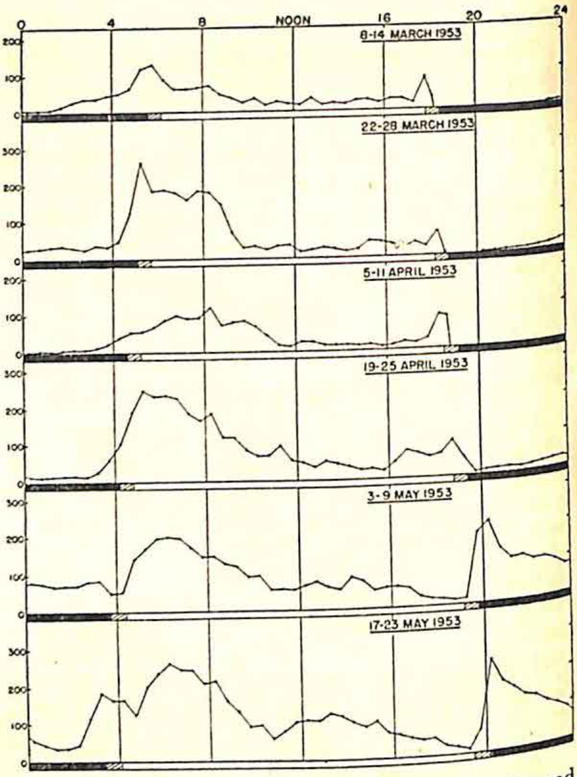

FIG. 2. Composite diurnal activity patterns of caged male *Zonotrichia leucophrys gambelii* for late winter and spring of 1953. Black bars designate the period of darkness; diagonally hatched bars, civil twilight; and open bars, the period between sunrise and sunset.

simultaneously, the raw daily data, in movements of the perch per half-hour period per bird, were transformed to percentage of total movements of the perch for the 24-hr. period. These transformed data were then used in all calculations to obtain a composite (four to six birds) daily activity pattern (transformed data) characteristic for the particular week. This pattern was then reconverted to an absolute basis by multiplication of the transformed datum for each half-hour period by the composite (four to six birds) mean total movements per bird per 24 hr. The data presented in Figures 1 and 2 represent adjusted mean activity patterns for four to six birds for a week. It must be emphasized that these patterns, although expressed in absolute units (movements of the perch per half-hour period per bird), must be regarded as indices because of the method of calculation and because the movements of the perches represent only a relatively constant (for a given bird in a given recording cage) fraction of the total movements of the bird. Table 1 gives the number of birds and the number of bird days used to derive each of the curves in Figures 1 and 2. The points on these represent the mean number of movements on the perch per bird for the particular half-hour period. These points are located at the centers of the spaces representing the half-hour periods except at the beginning and end of prolonged periods of activity. The mean time at which activity began or ceased determines the intercept of the curve with the base line. It should be noted that, in relation to twilight, there is a tendency to begin activity early in the morning and to end it early in the evening. This may have been the result of the better exposure of the cages to morning light than to evening light. On the other hand, a similar relationship was noted by Palmgren (14) with greenfinches (*Chloris chloris*) and bramblings (*Fringilla montifringilla*). It is obvious that, in both years, a typical *Zugunruhe* pattern had developed by May 1. Our field

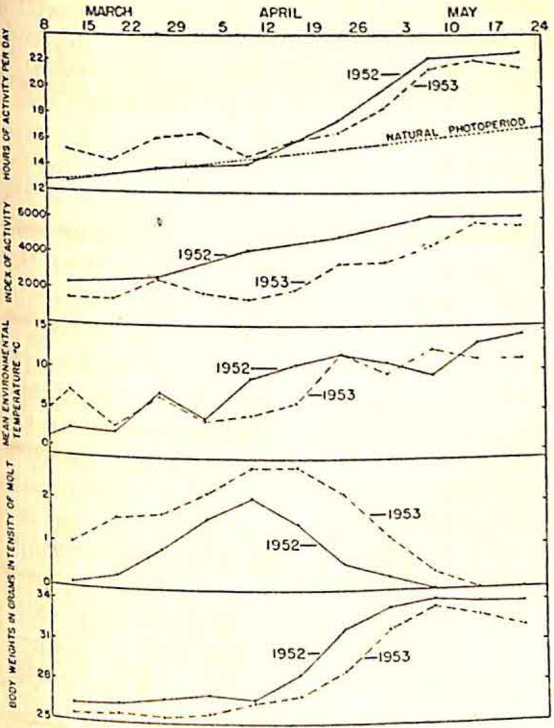

FIG. 3. Hours of activity per day, index of daily activity, mean environmental temperature, intensity of molt, and body weights of male *Zonotrichia leucophrys gambelii* in recording cages in late winter and spring.

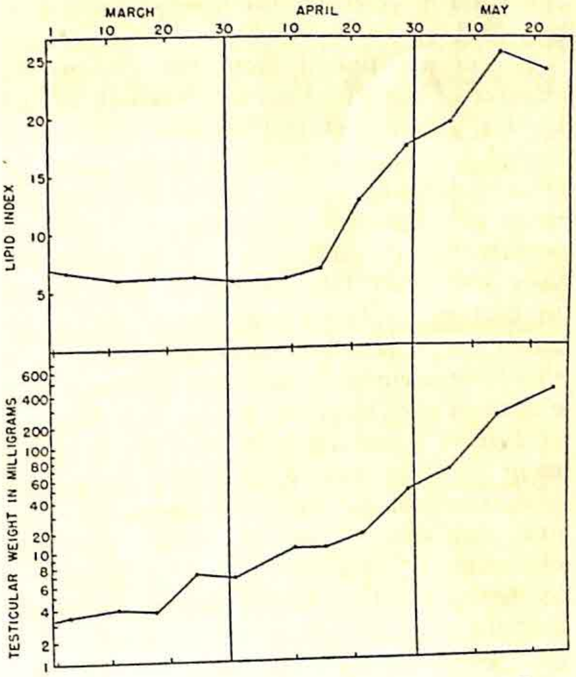

FIG. 4. Lipid indices and testicular weights of *Zonotrichia leucophrys gambelii*. A sample composed of birds collected in the wild, birds kept in large outdoor cages, and birds used in the recording cages in late winter and spring of 1952 and 1953.

observations indicate that migratory activity among the white-crowned sparrows in the Snake River Canyon began about the end of the third week of April in 1952 and 1953.

Of interest, also, is the number of hours of activity per day in relation to the natural photoperiod. These data are presented in Figure 3. They were obtained by calculating the mean hours of activity per day for the birds in the recording cages. Since, with a few minor exceptions, these birds were continuously active during daylight hours, the mean duration of night activity is represented by the displacement of the curves above the dotted line, which represents the duration of the natural daily photoperiod. The *index of activity* (Fig. 3) represents the daily rate of activity, i.e., the mean number of movements on the perch per bird per 24 hr. The *intensity of molt*, as represented in Figure 3, is simply based on the means of the arbitrary stages of molt. The *body weights* (Fig. 3) represent the means of the weights taken at the beginning and end of each one-week period.

For purposes of further comparisons, a series of data on lipid indices and testicular weights is presented in Figure 4. Included are data from birds collected in the wild, birds kept in large aviary cages, and birds used in the recording cages. No significant differences among these groups could be noted.

DISCUSSION

Although the primary function of this paper is to present a description of the vernal diurnal activity patterns in caged *Zonotrichia leucophrys gambelii* with particular attention to the development of *Zugunruhe*, certain additional observations and correlations appear worthy of comment. Caution must be applied in the assumption of causal relationships from these correlations, and, for the time being at least, in developing hypotheses concerning the development of migratory behavior on the basis of observations on *Zugunruhe*. *Zugunruhe* is probably best regarded as an expression, under very abnormal conditions, of a profound change in activity pattern which, in itself, is one facet of the complex of altered physiologic and psychologic processes of the migratory bird.

It appears patent from the changes in amount of nocturnal activity (as represented by the amount of displacement above the dotted line of the curves showing hours of activity per day in Fig. 3) that the development of *Zugunruhe* in spring is a gradual process which apparently has its inception very soon after the intensity of molt begins to decline. In this connection it should be noted that it is widely recognized (11, 21, 22) that migration and molt are mutually exclusive in most passerine species. Examination of Figures 3 and 4 reveals that the development of *Zugunruhe* is obviously associated with a gradually improving metabolic state and doubtless, therefore, with increased quantities of "productive energy" as conceived by Kendeigh (11). Among the factors which contribute to this improved metabolic state are the increasing environmental temperature, which results in decreased caloric requirements for thermoregulation, increased daily photoperiod, which at least theoretically allows more time for caloric intake, and the gradual decrease of molting activity. The extent of the caloric demands of molting in a small finch is evident from the investigations of Koch and de Bont (12), who found that the daily rate of metabolism increased as much as 33 per cent in a molting chaffinch (*Fringilla coelebs*). That there was, in fact, an improved metabolic state in our white-crowned sparrows is evident from the increase in body weights. We have unpublished data which allow us to conclude that these increases in weight (bottom of Fig. 3) are, to a substantial extent, the result of lipid deposition. This is supported by the data (Fig. 4) on actual lipid deposition as determined by extraction of carcasses of caged and wild birds taken during the period of the investigations. An increased deposition of fat, as an indicator of an improved metabolic state, is now generally associated with the initiation of *Zugunruhe* and natural migration (7, 13, 19, 25).

It seems apparent that in previous experiments (9) we have encountered an example of an increase in "productive energy" incident to improved environmental temperature. It was found that caged *Zonotrichia leucophrys gambelii* exposed to elevated environmental temperature (20° C.) in midwinter showed a pronounced increase in nocturnal activity. We have unpublished data which show that there was a concurrent increase in lipid deposition, indicating an improved metabolic state.

Doubtless the most important effect of the increasing daily photoperiod in spring is the activation of the anterior pituitary. The most spectacular and best known function of this activation is the marked increase in gonadotropic activity. Much of the available information on photoperiodic gonadal activation has been reviewed by Burger (5) and Benoit (1). The basic physiologic mechanisms are still not well understood, although progress has been made recently by studying the nature of the annual refractory period of the mechanism (2) and by investigations using intermittent light (10). That there was activation of the anterior pituitary in our birds concurrent with the development of *Zugunruhe* is evident from the concurrent gonadal development in caged and wild controls (Fig. 4).

It is tempting to assume a causal relation between the recrudescence of the testes (Fig. 4) and the development of *Zugunruhe* (Fig. 3). Indeed, this is the basis of several hypotheses of the mechanism of the stimulation of migration. For example, Rowan (18) and Bullough (4) have both described migration as a phase of sex behavior. The objections to the assignment of a primary regulatory role to the gonads in this regulation have been discussed at length by Farner (7). Although neither primary nor secondary gonadal regulation can or should be denied at this time, it is our opinion that the close correlation between gonadal recrudescence and the development of *Zugunruhe* or natural migration more probably indicates that both are the effects of more fundamental changes involving the anterior pituitary, at least in part. In other words, it appears desirable to seek explanations in terms of the nongonadotropic effects of the photoperiodically activated anterior pituitary.[4] Much interesting research remains to be done in order to understand these relationships. A study of the diurnal activity patterns of castrated migratory birds would be extremely interesting.

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[4] The possible roles of the nongonadotropic effects of the photoperiodically activated anterior pituitary and of nonpituitary effects of increased daily photoperiod in the regulation of migration are considered more extensively in "The Annual Stimulus for Migration: Its Physiologic Basis" by D. S. Farner, a chapter in *Recent Research in Avian Biology*, to be published by the American Ornithologists' Union in 1954.

SUMMARY

Caged male white-crowned sparrows of the migratory race *Zonotrichia leucophrys gambelii* display a pronounced increase in nocturnal activity (*Zugunruhe*) in spring. This occurs at the time of the normal migration of this race. The development of this activity pattern is gradual, having its inception at the time when the spring molt is becoming less intense and reaching its maximum development about the first week in May; it occurs during a period of gradually improving metabolic state, as indicated by increased fat deposition, and in the course of photoperiodically induced increasing pituitary activity as indicated by the developing testes.

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Received July 6, 1953.

HOARDING BEHAVIOR OF ADRENALECTOMIZED HAMSTERS[1]

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A survey of the literature on food hoarding reveals that there is a possible positive relationship between frequency of hoarding and level of activity (8). Since the goal of hoarding is not the accumulation of a pile of pellets (3, 5, 7), and since hoarding does not appear to follow a principle of least effort (4), some investigators have concluded that bodily activity per se is the goal of hoarding (2, 4, 5, 7). On the other hand, Waddell (10) has reported a study designed to test the bodily activity goal of hoarding. He concludes that the activity hypothesis is not supported. This experiment is by no means crucial, since the apparatus permitted the *S*s unlimited bodily activity.

From the many studies of food hoarding which have been reported, it may be noted that variation in the levels of activity of *S*s has been accompanied by changing rates of hoarding (8). Food deprivation raises the activity level and also tends to increase hoarding. A sharp decrease in environmental temperature has a similar effect. Mild emotional (anxiety) states increase activity and apparently have a similar effect on hoarding. Such variables as lighting the hoarding alleys, introducing social dominance, and using activity-depressing drugs appear to support a general positive relationship between amount of bodily activity and the frequency of hoarding food in the laboratory rat.

Several studies on the relationship of activity level to hoarding suggest themselves. Undoubtedly, a comparison of the frequency of hoarding with activity-wheel performance would indicate a positive relationship between these factors. A deliberate lowering of the animal's level of bodily activity should be followed by significant decreases in the frequency of hoarding. Lapetite and Soulairac (1) found that administering the antithyroxine drug, methyl thiouracil, to male rats resulted in a dramatically lowered food intake and frequency of hoarding.

Morgan and Stellar report:

> . . . that activity is not entirely controlled by one particular hormone is indicated by the reduction in activity that follows extirpation of the adrenal glands. In fact, the reduction is quite marked, being on the average about 90 per cent. . . . Increasing the quantity of salt fed to adrenalectomized animals, however, will produce a partial recovery of activity . . . (6, p. 374).

From the foregoing, it is reasonable to expect that extirpation of the adrenals would be followed by a marked decrease in the frequency of hoarding. Adrenalectomized *S*s which are supplied with a salt solution would be expected to hoard more than adrenalectomized *S*s which are not supplied with a salt supplement. The present study was designed to investigate these hypotheses.

METHOD

A total of 60 golden hamsters (48 males and 12 females) from the colony maintained by the Department of Biology at Bucknell University were used as *S*s. The general history of the colony has been given in an earlier report (9). All *S*s were experimentally naive and varied in age from 105 to 354 days at the start of the experiment.

The experiment was conducted in the laboratory room where the animals were housed. Five days before the hoarding trials began, *S*s were housed individually in cages of wood frame and wire mesh enclosure, 6 by 8 by 12 in. Alleys 3 by 3 by 10 in. were permanently secured to the living cages. Entrance to these alleys was permitted by the raising of a guillotine-type door. Food pellets and water were supplied ad libitum from weaning, and a daily ration of lettuce was supplied to all *S*s. Shredded newspaper was supplied in limited quantity for nesting. The temperature of the room ranged from 26° to 29°C.

Twenty-four hours before the first hoarding trial *S*s were placed on a deprivation diet of one food pellet (approximately 5 gm.) per day. This deprivation condition was maintained for all *S*s throughout the experiment, except for the sixth day, when the adrenals were extirpated. No trials were conducted on the sixth day. Thus, all test trials were conducted following a 24-hr. period during which the hamsters received only one food pellet, approximately 50 per cent of their normal consumption.

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[1] A version of this paper was presented at the 1953 meeting of the American Society of Zoologists.

Each evening at 7:00, the alleys were filled with pellets, and the hamsters were permitted to hoard for 15 min. At the end of this period, all pellets were removed from each cage and counted. The preoperative tests were conducted for five consecutive days.

The *S*s to be operated upon were treated as follows: (*a*) On the evening of the fifth day an area sufficiently large to make a 2-in. incision along the mid-line of the body was depilated. (*b*) On the evening of the sixth day each *S* to be operated upon was given a 1-cc. injection of a 1 per cent Seconal preparation intraperitoneally, and the adrenalectomy was performed. (*c*) The adrenals were assumed to have been completely removed if *S* succumbed in the expected period of five to six days. (*d*) Histological study was made of 12 of the 38 operated *S*s. It was found that the adrenals were completely removed in all these cases without complications.

Five more hoarding tests were conducted on days 7 to 11, constituting the postoperative period. Only 12 operated *S*s were supplied with a salt solution following adrenalectomy.

Two control groups were also used throughout the experiment. One consisted of 8 *S*s which were run through the five preoperative and five postoperative hoarding trials without intervening surgical insult. The second control group consisted of 14 *S*s which were subjected to sham adrenalectomies; i.e., the body cavity was entered and the adrenals were touched with a probe, but no adrenal tissue was removed.

Thus, a total of four groups of hamsters was used: group I ($N = 8$), normal; group II ($N = 14$), sham adrenalectomy; group III ($N = 12$), adrenalectomy supplied with a salt solution during the postoperative period; and group IV ($N = 26$), adrenalectomy not supplemented by salt solution.

RESULTS AND DISCUSSION

The basic results of the experiment are shown in Table 1. It may be seen that group III, the salt-supplemented adrenalectomized group, hoarded slightly more during the preoperative hoarding trials. A chi-square test of independence revealed no statistically significant difference among the groups in the preoperative hoarding tests.

A comparison for each group of the amount of hoarding in the pre- and postoperative periods indicates no significant differences for groups I and II, the normal and sham control groups. The salt-supplemented adrenalectomized *S*s (group III) decreased in hoarding frequency about 30.4 per cent ($p < .01$), while the nonsupplemented adrenalectomized group IV decreased in hoarding frequency approximately 33.5 per cent ($p < .02$). An examination of the results for group III indicated that all these *S*s hoarded less frequently following adrenalectomy, while only 16 *S*s of group IV hoarded less following adrenalectomy.

TABLE 1

Means and Standard Deviations of Total Number of Pellets Hoarded by All Groups

GROUP	*N*	PREOPERATIVE		POSTOPERATIVE	
		Mean	*SD*	Mean	*SD*
I. Normal control	8	40.2	17.1	49.9	14.1
II. Sham control	14	46.6	26.4	48.2	29.3
III. Adrenalectomy (salt supplement)	12	53.0	18.8	36.9	13.5
IV. Adrenalectomy	26	37.3	28.4	24.8	22.1

The results for the adrenalectomized groups support the hypothesis that adrenalectomized *S*s hoard less frequently, and by inference that decreasing the activity level of *S*s decreases hoarding frequency. It will be remembered that Morgan and Stellar (6) report a 90 per cent decrease in activity for non-salt–supplemented adrenalectomized *S*s. In the present study the amount of hoarding decreased about 34 per cent, although there were no apparent differences between the salt-supplemented and nonsupplemented groups.

As noted above, all *S*s in the nonsupplemented adrenalectomized group did not hoard less frequently, and all the members of this group succumbed within the expected time. It appears that a comparison of group means may serve to mask the actual relationship between frequency of hoarding and level of activity. In order to determine that bodily activity per se is the goal of hoarding, a study in which the level of activity of each *S* is compared with the frequency of hoarding should be done.

SUMMARY

This experiment was designed to determine the relationship between adrenalectomy and hoarding as an attempt to relate hoarding behavior to activity of the test organism. A total of 60 golden hamsters (48 males and 12 females) served as *S*s.

The *S*s were divided into four groups as follows: I, normal control ($N = 8$); II, sham control ($N = 14$); III, adrenalectomy with salt supplement ($N = 12$); and IV, adrenalectomy ($N = 26$). Hoarding trials were con-

ducted for five preoperative and five postoperative trials.

The results permit the following conclusions:

1. No significant differences were obtained among the various groups in preoperative hoarding.
2. No significant differences occurred between the normal control and sham control groups in pre- and postoperative hoarding performance.
3. A significant decrease of about 30 per cent was found in the postoperative performance of the salt-supplemented adrenalectomized group.
4. A significant decrease of about 34 per cent was found in the postoperative performance of the adrenalectomized (nonsupplemented) group.
5. Adrenalectomy clearly depresses hoarding behavior. It may be inferred that the activity level is reduced by adrenalectomy, and thus hoarding is affected. The relationship between hoarding and activity level still remains to be clearly demonstrated.

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Received July 10, 1953.

GENETICS OF HOARDING: I. *HOARDING DIFFERENCES BETWEEN HOMOZYGOUS STRAINS OF RATS*[1]

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In an investigation of hoarding activity in rats Morgan *et al.* (6) found that after 20 daily trials only 20 of 36 experimental rats reached the criterion of collecting five pellets during the 30-min. period. These were brown rats, descended from Lashley's original stock of crossed white and trapped wild gray animals. Several authors (5, 6, 9) have mentioned that, even under the most favorable conditions for eliciting hoarding, some rats will not exhibit this activity at all and others will collect only a few pellets during each trial. Most reports of hoarding studies do not specify the exact strain of rats employed, although heterozygous rats have been generally used. Marked differences in the hoarding performance of several strains of rats have been observed, regardless of sex differences. With albino rats, for example, it was found in a previous investigation (7) that on the fourteenth hoarding trial 39 per cent of the rats from a local laboratory line collected at least 11 pellets each, whereas 93 per cent of Sprague-Dawley rats hoarded more than 45 pellets each on this trial. In a subsequent investigation (8) it was observed that on the ninth trial 74 per cent of the Sprague-Dawley rats hoarded at least 20 pellets each, whereas on the same trial only 43 per cent of the rats from a Lippman strain collected this number of pellets. These observations lead to the hypothesis that the hoarding performance of rats may be determined, at least partially, by genetic factors.

Investigations concerning the genetic basis of behavior have recently been reviewed by Hall (3), who pointed out that behavior patterns such as spontaneous activity, emotionality, aggressiveness, and maze-learning ability are related to the genetic background of the animals. In most of these experiments the original groups of rats were not genotically pure, and the animals were then inbred for several generations on the basis of their performance in the investigated behavior. It has also been observed that strains of rats inbred for physical characteristics exhibited marked behavioral differences. Keeler and King (4), for example, found significant relationships between the coat color of rats and their temperamental behavior.

At the present time a number of inbred lines of rats with known genetic background can be readily obtained. An investigation of the hoarding performance of several of these strains may lead to a better understanding of the genetic basis of hoarding.

METHOD

Apparatus and Animals

Individual closed hoarding alleys were used. The home cage of each animal had a sliding door which, when opened, gave the rat access to a 40-in. long alley, at the end of which was a food bin containing a number of Purina Laboratory Chow pellets. The experimental room was uniformly lighted, and its temperature ranged between 68° F. and 74° F. The alleys were covered with aluminum paint in order to provide even illumination.

Three strains of rats derived from the stock of Dr. Dunning[2] were employed. These were highly inbred lines of rats with fur colors of black-hooded, brown-hooded, and solid brown Irish rats, respectively. The characteristics of these strains are shown in Table 1.

At the start of the experiment there were seven female and three male rats in each group. During the course of the experiment one male and one female brown-hooded rat died. The weights of the rats were recorded weekly, after the last deprivation trial, and at the termination of the experiment.

Procedure

Hoarding during deprivation. Five days before the start of the experiment the rats were weighed and placed in their individual home cages. During this period they were fed two pellets of the Laboratory Chow (approximately 15 gm.) daily. During the experimental period hoarding trials were generally con-

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[1] This investigation was supported in part by a grant from the Hixon Fund.

[2] The author is indebted to Dr. W. F. Dunning, University of Miami, Coral Gables, Florida, for providing the stocks of rats and to Dr. Ray Owen for breeding the animals.

TABLE 1

Characteristics of Strains of Rats Used in Experiment

STRAIN OF RATS	DUNNING'S DESIGNATION (LINE)	SUCCESSIVE GENERATIONS OF SIBLING MATING	FUR TYPE AND COLOR	HOMOZYGOUS FOR ANTIGEN	MEDIAN AGE* (DAYS)	MEDIAN WEIGHT* (GM.)	
						Female	Male
Black-hooded	August 35322	15	Nonagouti, black-hooded	D	265	200	315
Brown-hooded	August 990	49	Agouti, black-hooded	C	267	210	280
Irish	A × C 9935	45	Agouti, Irish	D	260	190	255

* At first hoarding trial.

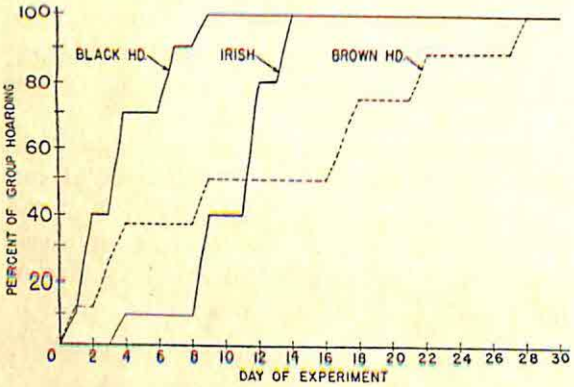

FIG. 1. Onset of hoarding for three strains of rats

TABLE 2

Summary of Hoarding Performance for Three Groups of Rats

STRAIN OF RATS	ONSET OF HOARDING (DAY OF EXPERIMENT)			HOARDING DURING DEPRIVATION (MEAN NUMBER OF PELLETS)			HD. DURING SATIATION (DAY WHEN HD. < 5 PELLETS)
	Mean	σ	Mdn	Mean	σ	Mdn	
Black-hooded	4.2	2.53	4.0	43.74	17.6	47	13
Brown-hooded	12.8	9.27	13.0	31.28	14.25	32	3
Irish	10.7	2.86	12.0	10.68	6.1	7	5

ducted at approximately 24-hr. intervals. Forty minutes before each trial each *S* was given two pellets in its cage. The sliding door was then opened for the 20-min. hoarding trial. All pellets were taken from the cage at the beginning and again at the end of each trial, at which time they were counted and returned to the bins. The number of pellets in the bin was adjusted to the magnitude of hoarding of each rat, but the maximum was 70. When a rat had collected 70 pellets, its hoarding trial was terminated, even if the 20-min. period had not yet elapsed. Although consecutive trials were usually conducted at daily intervals, they were sometimes two days apart. Under the latter conditions each *S* was fed two pellets on the intervening day. Hoarding trials under deprivation conditions were conducted until a rat had hoarded for 12 to 15 consecutive trials.

Hoarding during satiation. At the end of the last deprivation hoarding trial a pile of about 15 pellets was placed in *S*'s home cage. Hoarding trials were then continued according to the same schedule as under deprivation conditions. No pellets were placed in *S*'s cage at the beginning of the hoarding trial, however, and after the termination of each trial 15 pellets were left in the cage. The number of hoarding trials for the group of animals was between 5 and 15 except for two brown-hooded rats which had no hoarding trials under satiation conditions.

RESULTS

Onset of Hoarding

The experimental trials, during deprivation conditions, when rats in each group began to hoard are shown in Figure 1. One of the black-hooded rats started hoarding on the first day of the experiment, and the last one in this group did so on the ninth trial. The onset of hoarding for the Irish rats was consistently later than for the black-hooded ones. One Irish rat hoarded on the fourth trial, but the next one did not start until trial 9, and all animals in this group did not hoard until the fourteenth trial of the experiment. The brown-hooded group showed a great deal of variability in its onset of hoarding. One rat hoarded on the first day of the experiment, whereas the last rat in this group of eight animals did not commence hoarding until trial 28. The mean and median trials for the onset of hoarding of each group of rats are shown in Table 2. The significance of the difference between the means for the black-hooded and Irish rats was determined by computing its t ratio, which was 5.12 ($p < .001$). It may therefore be concluded that the black-hooded rats are superior in their onset of hoarding over the other two groups, because they commence hoarding earlier and exhibit less group variability than do either the brown-hooded or the Irish strains.

Hoarding during Deprivation

The daily mean hoarding scores for each of the three groups of rats during deprivation conditions are shown in Figure 2. In these curves the day preceding the onset of hoarding for each rat was taken as zero on the abscissa of the figure, and individual hoarding scores for each subsequent trial were then averaged for each group of rats. The hoarding curves in Figure 2 show clearly that the black-hooded rats hoarded consistently more than did the animals in the other groups. The mean and median hoarding scores for each group of *S*s during the 12-day hoarding period are shown in Table 2. For the difference between mean hoarding scores of black-hooded and Irish rats the *t* ratio was 5.42 ($p < .001$); for the difference between the scores of brown-hooded and Irish rats *t* was 3.58 ($.001 < p < .01$); whereas the difference between hoarding scores of the black-hooded and brown-hooded groups resulted in a *t* of 1.57 ($p > .10$).

The mean hoarding scores for the 12 trials show marked differences between the black-hooded and Irish groups of rats. One male black-hooded rat exhibited very little hoarding—its mean score for the 12 trials was only 4.4 pellets—whereas the next lowest hoarder in this group had a mean of 16.4 pellets during this period. Since several rats in this group often collected the maximum of 70 pellets in less than 20 min., their mean hoarding scores would have been considerably higher if they had been allowed to hoard all they could during the regular hoarding trial. The distribution of daily hoarding scores for individual rats in each group shows that 20 scores (from a total of 120) in the black-hooded group were 70 pellets, whereas there were only 3 such scores in the brown-hooded group, and only once did an Irish rat hoard more than 40 pellets. Hoarding scores of the Irish rats during this period show that no hoarding occurred 4 times (from a total of 120) during the 12-trial period and that the modal hoarding score was 2 pellets. The marked positively skewed distribution of hoarding scores for the Irish rats is indicated by its median of 7 and mean of 10.68 pellets. The median for the black-hooded *S*s was 47 pellets.

The hoarding data during deprivation trials indicate clearly the marked superiority of the black-hooded rats. The most significant differences were between the Irish rats and the two hooded groups, rather than between the two hooded groups of rats.

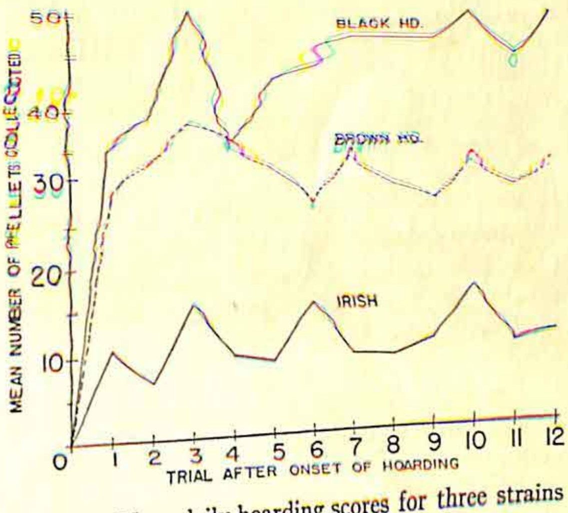

FIG. 2. Mean daily hoarding scores for three strains of rats during deprivation conditions

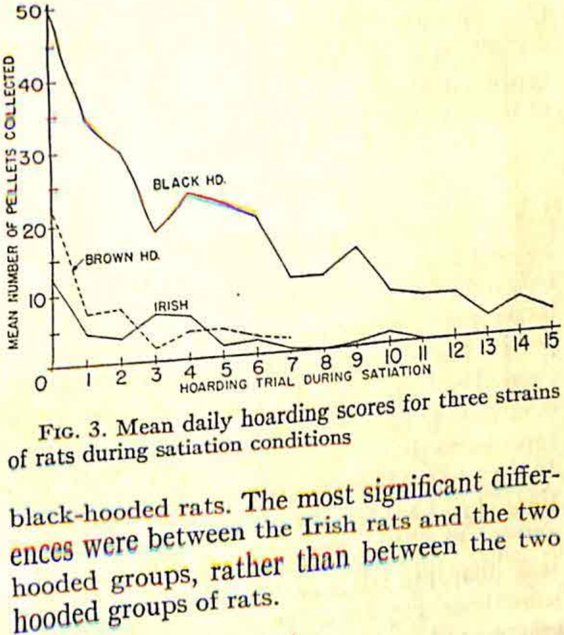

FIG. 3. Mean daily hoarding scores for three strains of rats during satiation conditions

Hoarding during Satiation

The hoarding curves during satiation conditions, shown in Figure 3, are for ten rats each in the black-hooded and Irish groups, but only for six brown-hooded rats, since two *S*s in the latter group started hoarding very late during the experiment. The hoarding activity of the brown-hooded and Irish rats became extinguished rapidly; *S*s in both groups had virtually stopped hoarding four days after pellets were placed in their home cages. The hoarding curve for the black-hooded rats, on the other hand, continues at a greatly reduced magnitude for several days after the end of deprivation conditions. Several rats in this group hoarded for 12 days during satiation conditions, and one rat still collected 36 pellets on the sixteenth trial.

Since there were relatively few rats in each group, the results cannot bring out variations in hoarding due to sex differences. Although one male black-hooded rat hoarded considerably less than did the other animals of its strain, the seven other male rats hoarded as well as did the females of their respective strains.

The weights of most rats reached minima at the time of onset of hoarding (an average reduction of about 15 per cent of the pre-experimental weights) and then increased slowly. Nearly all rats, regardless of strain or sex, had regained or surpassed their original weights at the end of the deprivation trials. Consequently, the reductions in hoarding during satiation cannot be ascribed to exceptional hunger conditions at the beginning of the satiation trials.

DISCUSSION

The hoarding superiority of the black-hooded rats over the other two strains was indicated by their earlier onset of hoarding, larger pellet collection during each trial, and persistence of hoarding during satiation conditions. Hoarding may be related to genetically determined behavior patterns such as spontaneous activity, as reported by Brody (1). In the present investigation incidental observations showed the black-hooded rats to be more active than the other animals. During satiation hoarding trials several black-hooded rats sometimes explored the alleys and tried to escape, although they did not collect pellets. The Irish rats, on the other hand, did not leave their home cages during this period, except when they occasionally retrieved pellets. It was also observed, while handling the animals, that the Irish rats acted more aggressively than did the hooded animals. When, after the termination of the experiment, the experimental rats were mated, it was found that a larger portion of the black-hooded females bore litters than did the Irish females, and that the litter size of the former was consistently larger than that of the latter.

These observations are not surprising since interrelations between several genetically based behavior patterns have been previously reported. Hall (2), for example, found that timid rats were more active, less proficient in maze learning, and less aggressive than were the more fearless rats. Moreover, Keeler and King, who found significant relationships between coat color and temperamental traits of strains of inbred rats, came to the conclusion that the same gene patterns were responsible for both. They stated that "the tame albino rat . . . was modified in morphology principally by the introduction of three coat genes, and in behavior particularly by the (non-agouti) black gene" (4, p. 249).

The results of the present investigation support the hypothesis that the hoarding performance of rats is, at least partially, determined by genetic factors. These factors may be expressed by phenotypical characteristics such as coat color and may also influence behavior patterns other than hoarding, such as spontaneous activity and aggressiveness. In order to clarify the genetic basis of hoarding behavior, investigations should be conducted with the progeny of the animals used in the present experiment. These may involve the offspring of matings of black-hooded with Irish rats, and the offspring of these heterozygous rats backcrossed with the original strains.

SUMMARY

Simultaneous hoarding tests were conducted with rats from three known inbred strains: a black-hooded nonagouti, a brown-hooded agouti, and an agouti Irish line. The following results were obtained.

1. The black-hooded rats started hoarding significantly sooner than did the other rats. The mean trial of onset of hoarding was 4.2 for the black-hooded, 12.8 for the brown-hooded, and 10.7 for the Irish rats.

2. The mean number of pellets collected during 12 days of hoarding under deprivation conditions was 43.7 for the black-hooded, 31.3 for the brown-hooded, and 10.7 for the Irish. The latter rats hoarded significantly less than did rats of the other two strains.

3. When hoarding was reduced by placing a pile of pellets in the rats' cages at all times, the brown-hooded and Irish rats virtually stopped hoarding after 4 days, whereas the

black-hooded rats collected an average of at least 5 pellets for 12 days.

It was concluded that the black-hooded rats were superior hoarders to the other animals. The genetic basis underlying hoarding may be related to other behavioral expressions, such as spontaneous activity and emotionality.

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Received July 27, 1953.

SEX DRIVE IN GENETICALLY HETEROGENEOUS AND HIGHLY INBRED STRAINS OF MALE GUINEA PIGS[1]

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The value of genetically homogeneous strains of animals for studies of behavior has long been recognized, but they are not commonly available and have not been used in most studies (5, 7). It has recently been possible, however, to develop a colony containing two highly inbred strains of guinea pigs, and a first contribution they have made to an investigation of hormonal, somatic, and psychological determinants of sexual behavior patterns is reported.

In 1906, 24 pairs of guinea pigs were set aside for the purpose of studying the effects of inbreeding (2). The animals were maintained wholly by brother-sister matings, but by 1917 most of the strains had died out or become so depleted that they were eliminated. Only families 2 and 13 are in existence today. It is estimated that during the years of inbreeding there have been approximately 80 generations of brother-sister matings. If, as Hall (5) and Russell (6) state, a high degree of homozygosity is reached after about 30 generations of brother-sister matings, families 2 and 13 may be considered to be genetically homogeneous.

Wright (8) and Eaton (2) reported a decrease in fertility. Eaton attributed the decrease to a higher percentage of sterile matings in some of the inbred families and to a decrease in litter size in others. The frequency of matings is also involved in fertility, but the importance of this factor was not estimated. This is explained partly by an absence of uniform criteria at the time of the earlier studies of what constitutes a mating, and partly by the lack of observations on the sexual behavior of the inbred animals.

The present study is concerned with the level of sex drive and the pattern of behavior displayed by the males of families 2 and 13 and a heterogenous stock observed as a control group.[2] A sufficient number of males was obtained from the two inbred families by making backcrosses, matings of cousins, and brother-sister matings. Crosses other than of brothers and sisters reduce homozygosity, but inasmuch as the strains were developed from approximately 80 generations of brother-sister matings, the reduction of homozygosity is not thought to have been great.

METHOD

Sixty-four males were used: 17 were from family 2, 18 from family 13, and 29 from the heterogeneous stock. Until weaning at about 25 days of age, the animals were caged with several other litters and their sows.

After weaning, some of the animals were isolated until testing was begun, whereas others were placed in cages containing males of the same age and isolated at least one week before tests were started. Equivalent proportions of inbred and heterogeneous animals were isolated or raised in groups.

The strength of sex drive of the male was determined by placing a female exhibiting a good lordosis in response to fingering (9) in a cage with the isolated male. His behavior was then observed for a 10-min. period. However, if an ejaculation occurred before the end of 10 min., the test was terminated because a male seldom shows any additional interest in the same female immediately after having ejaculated (4). During the test, six elements of sexual behavior were recorded: sniffing and nibbling, nuzzling, abortive mounting, mounting, intromission, and ejaculation (10). It is sufficient to note that *sniffing and nibbling* refers to what is perhaps a general exploratory behavior as the male comes in contact with the female. This contact may consist of sniffing, licking, or nibbling the female's hair with the teeth. *Nuzzling* designates sniffing and licking that is confined to the anogenital region of the female. *Abortive mounting* is scored when the male places one or both forepaws on the female, but does not bring his body into contact with hers. *Mounting* is used when the male mounts the female and brings his body into contact with hers, with or without accompanying pelvic thrusts. *Intromission* is self-explanatory and may take place with or without subsequent pelvic thrusts. When *ejaculation* occurs, the activity of the male is brought

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[1] This investigation was supported by research grant M-504 from the National Institute of Mental Health, of the National Institutes of Health, Public Health Service.

[2] Members of families 2 and 13 from which our stocks were developed were obtained through the courtesy of Dr. W. E. Heston, of the National Cancer Institute.

to an end with a grasping of the female and a convulsive drawing in of the flanks.

The score for a 10-min. test was obtained by weighting the behavior as follows: 0.1 for sniffing and nibbling, 0.2 for nuzzling or abortive mounting, 0.3 for mounting, 0.4 for intromission, and 0.5 for an ejaculation. Only the highest measure of behavior displayed in each 15-sec. period was scored. Therefore, if the test lasted 10 min., the maximum number of behavioral elements that could be scored was 40. If the test was shortened because of ejaculation, the score was multiplied by a factor which compensated for the shorter test period. This factor was the quotient of 40 divided by the number of 15-sec. periods up to and including ejaculation. With this procedure an animal that mated in the first 15-sec. period received the maximum score of 20, while an animal that did not come into contact with the female during the 10-min. test received 0.

For 18 of the males (6 from each of the three stocks), the score was the average of 15 tests; for 46 animals the score was the average of 10 tests. The animals were tested on the average of every sixth day (range, 3 to 10). The average age at the mid-point of the tests was 236 days for family 2 males, 227 days for family 13 males, and 240 days for the heterogeneous males. The diet consisted of commercial rabbit pellets, oats, alfalfa hay, green vegetables, and water. The temperature of the laboratory was uniformly 70° to 75° F.

RESULTS

The sex drive scores for the inbred and heterogeneous animals are summarized in Table 1. It is evident that the strength of sex drive of both inbred families was significantly lower than that of the heterogeneous group. In addition, the inbred animals presented a much more homogeneous picture. This is reflected in the lower standard deviations. The variances of both inbred families were significantly lower than the variance of the heterogeneous animals.

The average scores of the two inbred families differed only insignificantly. We would note however, that the same average score could be achieved in several ways. For example, an animal could achieve a certain score by displaying little mounting, few intromissions, and no ejaculations, but by exhibiting a large amount of the less mature sexual behavior (sniffing and nibbling, nuzzling, and abortive mounts). The same score could also be achieved by an animal that ejaculated without displaying much other behavior. For this reason, an analysis was undertaken to determine whether these families had characteristic patterns of sexual behavior.

TABLE 1

Average Sex Drive Scores, Standard Deviations, and Relevant Significance Tests for Family 2, Family 13, and Heterogeneous Male Guinea Pigs

	N	NUMBER OF TESTS	AVERAGE SEX DRIVE SCORE	STANDARD DEVIATION	INBRED VS. HETEROGENEOUS GROUP	
					Variances	Means*
Family 2	17	200	4.95	1.44	$F = 4.07$ $p < .02$	$t = 5.03$ $p < .01$
Family 13	18	210	4.75	1.08	$F = 4.52$ $p < .02$	$t = 5.50$ $p < .01$
Heterogeneous group	29	320	7.48	2.30		

* Inasmuch as the variances are significantly different, the t tests were performed in accordance with the approximation method suggested by Edwards (3).

In order to compare patterns of behavior, the scored behavior was reduced to frequency of occurrence per minute (Table 2). In so doing, allowance was made for the fact that an animal that mated more frequently would have had less time with females because the tests were always terminated following a mating. In order to calculate frequency rates the scored behavior of each type was totaled for all the animals of a family. This sum was then divided by the total minutes of testing for that family. The data summarized in Table 2 indicate that family 2 males tended to be more active. They achieved a rate of 2.63 for total scored behavior, whereas the rate for family 13 males was 2.40. While this difference between the inbred families is not significant, the possibility that family 2 males may be the more active is indicated.

With the exception of the component sniffing and nibbling, family 2 males showed a higher rate of activity for behavior below the category of mounting, while family 13 males exhibited a higher rate of activity for mounting, intromission, and ejaculation. These differences are significant at the .03 level or better for nuzzling, abortive mounting, mounting, and ejaculation and show a similar trend for intromission ($p = .097$). A comparison of frequency of ejaculation in rates per minute, although presenting significant differences, is not as meaningful as a comparison of the percentage of the total tests that had ejaculations. Ejaculations occurred in 7 per cent of the tests with family 2 males and in 16.5 per cent of the tests with family 13 males.

TABLE 2

Frequency per Minute of Scored Behavior

	SNIFFING AND NIBBLING	NUZZLING	ABORTIVE MOUNTING	MOUNTING	INTROMISSION	EJACULATION	TOTAL SCORED BEHAVIOR
Family 2 ($N = 17$)	0.797	1.089	0.465	0.162	0.107	0.007	2.627
Family 13 ($N = 18$)	0.839	0.731	0.287	0.346	0.174	0.019	2.396
Significance of differences	$t = 0.22$ $p > .05$	$t = 2.84$ $p < .01$	$t = 2.24$ $p < .03$	$t = 2.63$ $p < .02$	$t = 1.30$ $p > .05$	$t = 2.50$ $p < .02$	$t = 1.01$ $p > .05$

The present investigation provided an opportunity to cover an omission in the description of the method for measuring strength of sex drive given earlier (10). Inasmuch as only the highest behavior displayed in each 15-sec. period was being scored, it was obvious that some behavior was without effect on the score. To meet this objection, an analysis was made of all the behavior exhibited by 12 animals (6 each from families 2 and 13) during testing in this study, regardless of whether it had been used in calculating the score. The results were not appreciably different from those obtained when only the highest behavior in each 15-sec. period was scored.

In 1932, when Eaton (2) reviewed the data collected on the inbred guinea pigs, he reported that the birth weight of the young successfully raised and the gain in weight up to the time of weaning were lowest in family 2 animals. Of the families in existence at that time, family 13 was among the highest in these two respects. After 21 additional years of inbreeding, this difference is still pronounced. Raised under the same conditions, the average birth weights of family 2 and family 13 males are 81.5 and 92.9 gm., respectively, while their average weights at the time of weaning are 195.9 and 232.8 gm. These differences are significant ($t = 1.98$, $p < .03$, for the birth weight, and $t = 2.49$, $p < .01$, for the weaning weight).

Our data reveal the continued existence of another difference reported by Eaton. In 1932, family 13 had the highest percentage of abortions, defined as cases in which all the fetuses were born dead before the sixty-third day of pregnancy. In the tests in this study, abortions occurred in 28.5 per cent of the 40 fertile matings in family 13, whereas no abortions occurred in 17 matings between family 2 animals.

DISCUSSION

The homogeneity of performance found in two highly inbred families emphasizes the value of such animals for studies of sexual behavior. In contrast, the larger interindividual variance of the heterogeneous animals necessitates the use of very large groups in order to ascertain the role of hormonal and experiential factors which may be contributing to the development of sexual behavior, but whose effect might otherwise be concealed by the differences between animals. On this point Scott states that with closely inbred strains of animals, "Hereditary variability may be considered a negligible quantity, and this may in some cases greatly reduce the numbers required for sampling and for obtaining clear experimental differences" (7, p. 529).

The homogeneity of the inbred animals appears to have a genetic basis, but alternative explanations cannot be excluded without further study. Eaton (2) noted that a control stock maintained by matings of animals more distantly related than third cousins had suffered a decline in vigor that was equal to, and in some instances greater than, that of the inbreds. This indicated that some influence aside from inbreeding was responsible for the loss of vigor. It is possible, therefore, that some cumulative effect associated with caging, and independent of breeding, may have been operating. Since 1906 the inbred animals have been maintained under special conditions which restricted their contact with other animals. This was necessary in order to limit matings to brother-sister pairs. The heterogeneous animals used in this study, on the other hand, were maintained in large breeding cages prior to the time they were acquired by the laboratory. It would be difficult to determine the cause of the changes which occurred in the inbred animals, but such factors as nutrition, cage space, activity, and the amount and type of contact with other animals may be relevant.

On the other hand, factors of special handling cannot explain all the results found in this study. Families 2 and 13 received similar treatment over the course of years, but they have responded differently. The families not only have characteristic weight curves and abortion rates, but evidence has been presented which indicates that they have characteristic patterns of sexual behavior.

At present, these inbred families are being utilized in experiments which are designed to assay the role of experience, hormonal stimulation, and nutrition for the development of sexual behavior.

SUMMARY AND CONCLUSIONS

Two highly inbred strains of male guinea pigs were tested for strength of sex drive. The average scores of the inbred families and a heterogeneous stock were compared.

1. Males from the inbred strains were significantly lower in sex drive and had significantly smaller variances than the heterogeneous animals.

2. The males from the inbred families achieved approximately the same score, but displayed different patterns of sexual behavior. Family 2 males were more active but displayed less mature sexual behavior than family 13 males.

3. Although alternative explanations cannot be excluded, the possibility that the character of mating behavior may have a genetic basis is suggested.

4. The inbred families had characteristic growth curves and characteristic rates of abortion that were similar to those reported 21 years earlier.

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Received July 17, 1953.

THE GENESIS OF EMOTIONAL BEHAVIOR: AN EXPERIMENTAL STUDY OF THE DOG

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Earlier studies on the genesis of emotional behavior (1, 2, 8) have indicated that emotional development occurs in a specific, patterned sequence. While these data have been used as evidence for the role of maturation (4, 7), they describe, in fact, the product of an *interaction* of environmental stimuli and sensory and neural maturation.

Recent experimental studies of spontaneous fears in the chimpanzee by Hebb (5) and Riesen (6) have shown that early visual experience is necessary for the emergence of this type of behavior. Furthermore, Melzack (11) has provided evidence that the integrated part of an emotional response (i.e., attack or retreat) is dependent in part on learning processes.

The present investigation is an attempt to answer the following question: If an organism is deprived of normal sensory experience, but neural and sensory maturation is not otherwise disturbed, how would its emotional behavior compare with a normally reared individual of similar heredity?

METHOD

The method of experimental sensory restriction has been described in an earlier paper from this laboratory (3). Typically, two littermate dogs were reared from puppyhood to maturity in a cage which was so designed that the dogs could not see outside, although normal daylight was able to pass through the top.

After the restricted dogs were released, they received the same amount of handling and sensory stimulation as their normally reared littermates.

Subjects. Four litters of an inbred Scottish terrier strain were used. Each litter was randomly divided into two groups. One group, containing a total of nine dogs, was placed in restriction cages. The second group, containing eight dogs, was reared in a "free environment": two dogs were raised in private homes, while the others remained in the laboratory and received considerable handling.

Three litters were tested three to five weeks after the restricted dogs were first released. Two of these litters were tested a second time ten months after release. The fourth litter received preliminary tests two months after release and was retested ten months later.

Apparatus. Seven innocuous but emotion-provoking objects (11) were used: a mannequin head, a bear skull, a chimpanzee skull, a toy car, an umbrella, a balloon, and a live rabbit.

Procedure. The experimental procedure was the same for both groups. Each dog was led into a room which was lighted by a lamp, under which lay the test object. After 60 sec., the object was moved slowly, in zig-zag motion, toward the dog for another 60 sec. The umbrella was opened to a 36-in. spread, and the balloon was blown up to 10 in. in diameter, over a period of 30 sec., before being moved toward the dog. Behavior was recorded only before the rabbit made its first movement.

Categories of emotional behavior. The emotional responses of the dogs were recorded under three headings: diffuse emotional excitement, avoidance, and aggression. This classification was made in consultation with others who were working with the dogs and presented little difficulty in evaluating the emotional responses obtained in the present experiment.

The behavior which was tabulated as *diffuse emotional excitement* was characterized by increased excitement when the stimulus object came into the dog's field of vision: *S* would move about rapidly, sometimes in a whirling motion, but always keep a certain distance from the object. It was also recorded when a type of behavior occurred which can be best described as "teasing" or "stalking," with gross, excited body movements: the animal would jump back and forth near the stimulus object, and although rudimentary forms of avoidance and aggression could be discerned, the excitement often increased without the emergence of either pattern.

The two types of behavior which were classified as *avoidance* were: (*a*) a characteristic response in which the animal squats, has its ears pressed against its neck, and has its head turned so that the object is always 90° or more from the dog's line of vision; and (*b*) excited withdrawal when the object was moved toward the dog. Frequently the dog lowered its body quickly and then moved excitedly away from the test object.

Aggression was usually displayed by an excited approach toward the stimulus object by the dog, accompanied by growling, barking, snapping, and sometimes biting.

The dogs were numbered randomly by the animal caretakers, and *E* was unaware of the past history of the individual animals.

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[1] The author wishes to acknowledge gratefully the advice and guidance of Dr. D. O. Hebb. The help of Mr. W. Ponman in rearing some of the dogs, and of Mr. J. D. Cleghorn in supplying some of the test objects is also greatly appreciated. This research was assisted by grants from the Dominion-Provincial Mental Health Program and the Rockefeller Foundation.

RESULTS

Only one type of response was recorded for each dog to the presentation of a test object. The responses of all the dogs to the seven objects were ranked with respect to category of emotional behavior and past history of the dog. The nonparametric U values, described by Mann and Whitney (10), were then calculated, and p values were obtained for differences between the free and restricted dogs.

Results obtained three to five weeks after the release of the restricted dogs. The dogs which were reared in restriction cages made significantly more responses in the category of diffuse emotional excitement than the free-environment dogs (Table 1). The free-environment dogs, however, made significantly more avoidance responses. The probability that these differences would occur by chance is .001. Only one aggression response was recorded.

Qualitative differences between the two groups were observed. The avoidance of the free-environment dogs was usually performed by a selective, clearly adaptive movement, while the occasional avoidance response of the restricted dogs involved "mass activity" and more excitation, with the whole body participating in the response.

Results obtained 10 to 12 months after the restricted dogs were released. The restricted dogs still made significantly more responses in the category of diffuse emotional excitement. However, the avoidance responses of the restricted dogs increased in frequency, and there was no longer a difference between the two groups in this category. But the free-environment dogs now displayed aggression responses, which differed from the behavior of the restricted dogs at the .026 level of significance.

TABLE 1

Frequency of Various Forms of Emotional Response by "Restricted" and "Free" Dogs in Seven Tests

RESPONSE	3 TO 5 WEEKS AFTER RELEASE			10 TO 12 MONTHS AFTER RELEASE		
	RESTRICTED	FREE	p	RESTRICTED	FREE	p
Excitement						
Mean	3.9	0.5	.001	1.6	0.2	.045
Range	2–7	0–1		0–5	0–1	
Avoidance						
Mean	1.9	5.5	.001	4.0	3.5	—
Range	0–4	5–6		2–7	0–6	
Aggression						
Mean	0	0.2	—	0	2.2	.026
Range		0–1			0–7	
No emotional response						
Mean	1.3	0.8	—	1.3	1.2	—
Range	0–3	0–2		0–4	0–2	

Observations of restricted dogs in their cages. Although the restricted dogs received a narrow range of sensory stimulation, they apparently acquired thorough familiarity with these stimuli. During the period of restriction, any small change in their cages, such as a new object on the wall or the removal of a fixture from the cage, was sufficient to cause great excitement. But within periods of less than 10 min. the dogs would sit down at the part of the cage which was farthest from the new object, and with their backs to it. They would occasionally move their heads toward the object, but then quickly turn away and face the opposite direction. This undisturbed avoidance often lasted for days.

When the restricted dogs were first released, however, their level of excitement was higher than any yet observed in the normal controls, and was maintained for long periods of time. But the dogs became quiet immediately if they were returned to their cages for a short time between testing periods.

The emergence of avoidance from diffuse excitement was observed occasionally during a single test trial. The dog pranced rapidly back and forth near the test object until, at the end of the trial, it moved backward only after every movement of the object.

DISCUSSION

The present investigation adds further support to the view that diffuse emotional excitement is a primitive, disturbed response out of which avoidance and other forms of emotional behavior develop (2, 6). It demonstrates, however, that this behavior is primitive only in so far as it appears prior to integrated forms of emotional behavior. It may appear at any stage of the animal's life when the situation differs greatly from any that the animal has already encountered.

The behavior of the restricted dogs in their cages indicates that sensory and neural maturation had provided the necessary substrate for the restricted dogs to react adaptively. It seems, therefore, that well-organized experience of the environment in which emotion-provoking objects will appear is necessary for the emergence of adaptive emotional behavior such as avoidance and aggression. The fact that considerable diffuse excitement was manifested by the restricted dogs after almost a year of normal laboratory environment indicates that organized perceptual experience of a new environment is acquired through long, continued periods of sensory stimulation. The present experiment also provides evidence that in the course of emotional development avoidance appears before aggression.

It can be concluded from the results, then, that the degree to which an organism is disturbed by innocuous, emotion-provoking objects is determined, in part at least, by (*a*) the range of experience of the organism, (*b*) the degree of familiarity which the organism has with the environment in which the disturbing stimulus appears, and (*c*) the magnitude of change in the environment. Thus, if spontaneous fears are to be used as a valid test among different species, as suggested by McBride and Hebb (9), these contributing factors must be kept constant.

Furthermore, observations of restricted dogs in their cages indicate that results obtained with restricted animals do not represent simply the effects of a deficiency of sensory experience. They also reflect a disruption of organized behavior which the animal can perform if it is observed in the more familiar environment of its home cage.

SUMMARY

1. Four litters of Scottish terriers were divided into two groups. One group was reared in a restricted environment. The other group was raised in homes or in a normal laboratory environment. After the restricted dogs were released, both groups were tested with seven innocuous but emotion-provoking objects.

2. The restricted dogs, three to five weeks after they were released, showed a predominance of diffuse emotional excitement, while the control dogs tended to avoid the test objects.

3. The restricted dogs, 10 to 12 months after release, made as many avoidance responses as the free-environment dogs. While the restricted dogs continued to manifest diffuse emotional excitement, the free-environment dogs now displayed aggression responses.

4. Well-organized experience in the environment in which emotion-provoking objects will appear is necessary for the emergence of adaptive emotional behavior such as avoidance and aggression.

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Received May 13, 1953.

THE DISCRIMINATION BETWEEN LIGHTS OF DIFFERENT WAVE LENGTHS IN THE CAT

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Most theories dealing with the physiological mechanism of color vision emphasize the role of the retina in the discrimination between lights of different wave lengths. Animals whose visual receptors respond differentially to such lights are assumed to have color vision, whereas those whose visual receptors give equal responses are unlikely to have color vision.

By the use of the microelectrode technique, Granit (6) examined the retinal sensitivity of a large number of animals to lights of different wave lengths, and found differential retinal sensitivity under conditions of light adaptation in animals that hitherto had been considered totally color-blind. He points out that in animals for which the existence of color vision had been well established, he invariably found a broad dominator band, representing "brightness," as well as some narrow modulator bands, representing "color," in various spectral regions.

By modifying his technique, i.e., by selectively adapting the cat retina to lights of different wave lengths, Granit (5) was able to isolate narrow response curves (modulators) with sensitivity maxima in the red (λ600 mμ), the green (λ520–540 mμ), and the blue (λ440–460 mμ) region of the spectrum. Since color vision may be assumed to exist in an animal if it has shown to exercise a choice between colors on the basis of wave length under controlled conditions, the present experiment was designed to determine by behavioral technique to what extent this retinal mechanism of wave length discrimination is linked to an ability on the part of the animal to make use of the signals received from the retina, so as to be able to respond differentially.

METHOD

Discrimination Apparatus

The apparatus employed in the experimental situation was almost identical to that employed in the previous investigation on the animals' photopic spectral sensitivity (11), and a detailed description and a diagram of the apparatus are given in an earlier paper (9).

The apparatus consisted essentially of a Y-shaped discrimination box which had two doors, one on either arm of the Y. The stimulus light was projected from behind onto a 3-in. by 3-in. opal glass panel placed in the middle of each door. This stimulus panel was surrounded by white material of high reflecting power. The animal signified its choice by pushing open one of the doors; it obtained its food reward behind the door bearing the positive stimulus.

Light Adaptation

Prior to the daily experiments all animals were light-adapted for at least 30 min. Light adaptation during the course of the experiments was maintained by high over-all illumination and by eight 100-w. lamps suspended along the length of the experimental apparatus. Four additional 100-w. lamps were suspended above the restraining compartment of the apparatus to which the animal was returned after each run. In no part of the experimental situation was the over-all intensity below 300 ft-c.

Control of Pupil Diameter

The high light intensity used for keeping the animals light-adapted produced a contraction of the pupil to a narrow slit. In order to check on the effect of this function on light adaptation, four animals (two of each group) were tested in the discrimination of green versus red and green versus blue, while the animal's pupil was kept open by drops of homatropine administered locally before the beginning of the experiment. They were given 900 trials to each of the two pairs of colors.

The Stimulus

Ilford spectrum filters No. 601–608 were used to provide the spectral stimulus. These filters have their

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The author gratefully acknowledges the help given by Dorothy Howard and A. Merrick whose conscientious handling of the animals greatly contributed to the success of this work. The writer's colleagues, both in England and in the United States, gave many valuable suggestions. Special thanks are due to Dr. Karl H. Pribram for his active help in the preparation of this paper.

regions of maximum transmission in the violet, blue, blue-green, green, yellow-green, yellow, orange, and red part of the spectrum, respectively. The spectral transmittance of all spectrum filters used was determined by means of a Beckmann spectrophotometer, and the relative energy content of the filter-source combinations was computed.

The spectral stimuli were projected onto the stimulus panel in the doors of the discrimination apparatus. The stimulus intensity could be varied by means of neutral density filters and optical wedges in the manner described in an earlier paper dealing with the determination of the animals' photopic spectral sensitivity (11). The spectral transmittance of the optical wedges and of samples of the neutral density filters employed was determined by means of a Beckmann spectrophotometer. Their neutrality—over the visible range—was found satisfactory. Prefocus projector lamps, 230 v. 250 w., with a color temperature of approximately 3000 K were used as light source, and their intensity—with no filters in the beam—was kept constant at 200 ft-c; the measurements were made at the stimulus panel.

Optical System and Voltage Control

The arrangement used for the present experiment was essentially identical to the one used in previous investigations (9, 10).

Subjects

Eight animals were used in the present study. The experimental group consisted of four animals whose spectral sensitivity had been determined in previous experiments (10, 11). The control group consisted of four animals that had never been tested.

Procedure

For the determination of the animals' photopic spectral sensitivity, the intensity of the white-light stimulus was kept constant while the simultaneously presented spectral stimulus was changed in intensity until the animals could no longer discriminate between them. By this method eight spectral regions, isolated by Ilford spectrum filters, were matched by the animals to a constant white light. These data afforded a measure of the relative amounts of spectral lights that the animals confused with the constant white-light stimulus. These various relative amounts of the eight different spectral lights, having led to a constant response on the part of the animals, are, therefore, of equal brightness value to the cats. Any discrimination between spectral stimuli thus matched in brightness may be assumed to be based on differences in wave length and is suggestive of color vision.

The various spectral stimuli were presented on the stimulus panel in random pairings in successive trials. All animals were trained for 950 trials with each pairing of the eight spectral filters.

Five hundred additional trials were obtained from all animals to the spectral regions isolated by the following three filter combinations: blue (+) versus red, green (+) versus red, and blue (+) versus green.

One of any two spectral stimuli was arbitrarily called positive and rewarded, and the position of this stimulus on the panel was interchanged with that of the negative stimulus in random order. The intensity of the negative stimulus in each pair of filters was changed by a small amount in random steps in each series of ten runs, so that the animal was prevented from learning to respond to any small brightness difference that it might still detect between the two stimuli. In each daily experimental session we aimed at obtaining 50 responses from each animal.

During the course of the experiments the animals could not obtain the food behind the door bearing the negative stimulus color; they were not allowed to correct for a wrong and unrewarded response by turning back and opening the positive stimulus door to obtain their reward. Later, the method was changed, and the animals were allowed to correct themselves for any mistake. With both these methods, however, occasional unresponsiveness and a marked tendency for the animals to fall into a persistent "position habit" were observed.

Control Experiment

As stated above, the animals employed in this investigation had all been used previously in determinations of spectral sensitivity. These experiments, based on discrimination between differences in intensity, may have ingrained the brightness habit to such an extent that the animals may have been quite unable to "switch over" and respond to differences in wave length of the stimulating lights. For this reason four fresh animals with no previous training in any sort of discrimination were introduced into the experimental situation to determine if they would learn to discriminate between the spectral stimuli to which the other cats had given responses of equality in brightness. The stimuli were presented in the same manner as for the experimental group. When after 950 responses to the stimulus combinations blue versus red, blue versus green, and green versus red, the responses remained random, their learning ability was checked in a brightness discrimination experiment (red [+] versus white light of high intensity). All the control animals learned this discrimination to a criterion of 16 correct responses in 20 runs in an average of 200 trials. When the red-light stimulus was exchanged for blue or green light, there was complete transfer of correct responses to these stimuli, provided the white-light stimulus was of much greater relative intensity.

RESULTS

None of the experimental animals conformed to a learning criterion of 80 per cent correct responses in a series of 20 runs within 950 trials. After an additional 500 trials to three of the spectral regions previously explored, none of the animals showed any evidence of learning. Figure 1 shows—as an indication of the general trend—the responses to a red (+) versus green (○), and blue (+) versus yellow discrimination (X). Plots of results of discriminations between the other color pairs are all of a similar character.

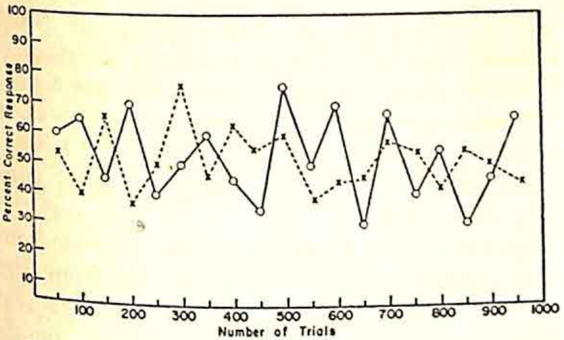

FIG. 1. Learning curves (mean) of four experimental animals for discriminations between colors of equal brightness: red (+) versus green spectral light stimuli (O), blue (+) versus yellow spectral light stimuli (X). Each point is the mean of 50 responses. Plots of the responses to the other pairs of spectral stimuli were all of the same general character.

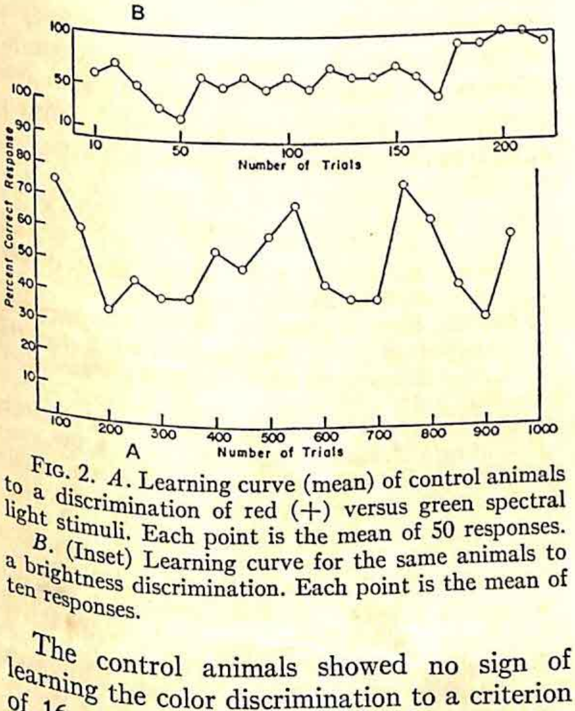

FIG. 2. *A*. Learning curve (mean) of control animals to a discrimination of red (+) versus green spectral light stimuli. Each point is the mean of 50 responses. *B*. (Inset) Learning curve for the same animals to a brightness discrimination. Each point is the mean of ten responses.

The control animals showed no sign of learning the color discrimination to a criterion of 16 correct responses in 20 runs after 950 trials (Fig. 2*A*). Figure 2*B* shows the responses of the same animals to a brightness discrimination that was learned after about 200 trials.

The responses of the animals whose pupils had been dilated by the local application of homatropine did not differ significantly from those of the experimental group. They also gave only chance performance in 900 trials.

DISCUSSION

In previous investigations on the same animals, their spectral sensitivity had been determined for scotopic (10) and photopic (11) levels of illumination. It was observed that, in spite of a very large number of reinforced trials, there was for each animal a certain intensity level of colored light which it confused with the white-light stimulus of constant intensity. (In a modified form of the experiment, a certain intensity level of white light was found which all animals confused with the spectral stimulus when this was kept constant.)

This observation, as well as the complete ease with which all animals transferred their responses from one color to any other, provided the opposing stimulus on the panel was sufficiently higher in intensity than the white light, gave some indication of the possible absence of color vision in this species. The inability of the animals in the present study to discriminate between colors on the basis of wave length when the spectral stimuli are matched in brightness, and the inability of the control animals to learn this discrimination afresh, fits in well with other available evidence where this species was examined for color discrimination by the method of behavior (2). De Voss and Ganson (3), who trained cats to respond to colored papers, found for each of the colored stimuli a certain gray paper that the animals confused with it. Essentially, the same result is reported by Gregg *et al.* (8), who found that their cats were unable to discriminate between spectral lights produced by filters when white light of varying levels of intensity was introduced.

The only positive result obtained by the behavioral technique is claimed by Kalischer (12). His procedure, however, is open to grave objections. In training the animals to undyed versus dyed food, he made no attempt to control olfaction, and further he gives no details with regard to his control of the brightness factor.

The application of the method of conditioned reflex to the problem of animal color vision has yielded negative results for Pavlov (13) on the cat; while for the rabbit, Brown (1) claims to have established this function.

The evidence obtained by Granit (6) for a peripheral mechanism of wave-length discrimination in the cat is corroborated by Donner (4), who investigated the impulse frequency at "on" and "off" in 100 elements of the cat's eye. He found that in elements which were selectively sensitive to wave lengths, the response to red rose at a faster rate than the response to green. The late maximum for the blue stimulus he considers characteristic for that color. Donner then traced his curves through the spectrum and found three maxima, one each at λ600 mμ, λ520 mμ, and λ460 mμ, thus corresponding to the maxima of modulators found by Granit (6) in the same eye. The same areas of predilection reappeared when color reception was examined by the method of polarization (7).

The evidence for lack of any color discrimination in the cat, as determined by behavioral criteria, raises a question as to the significance of modulator curves. It may be possible for differential retinal sensitivity to exist with no mechanism for central analysis of the messages from the ganglion cells. Furthermore, the modulator curves may not represent the significant neural messages in any case.

SUMMARY

The ability of cats to discriminate between lights of eight different spectral regions was examined by the use of the method of behavior in the discrimination box.

In order to ensure that the discrimination was not based on brightness but on differences in wave length, the various relative amounts of different spectral lights that, in a previous investigation on the animals' photopic spectral sensitivity, were found to be of equal stimulus value to the animals were used as stimuli and projected in pairs.

By definition, color vision can only be assumed to exist in an animal if it has shown to exercise a choice between different spectral lights, depending on wave length.

Thus, the conclusion that color discrimination seems absent in this species is based on the following observations:

The four experimental animals were unable, after 950 trials, to discriminate between lights of different wave lengths when these had been matched in brightness by the animals themselves. An additional 500 trials to three selected spectral regions also produced no evidence of learning.

Four control animals, untrained in any sort of discrimination, were introduced into the stimulus situation to determine if they could discriminate, on the basis of wave length, between spectral lights which had been matched in brightness by the experimental group. No learning was evident after 950 trials. When the learning ability of these animals was tested in an intensity discrimination, all animals learned to discriminate a low-intensity spectral stimulus from a white light of relatively high intensity within 200 trials.

In order to test the effect of pupil constriction (due to light intensity) on the response of the animals, four cats (two from the experimental group and two from the control group) were run for 900 trials to two sets of spectral stimuli with their pupils dilated by local application of homatropine. The responses of these animals did not differ significantly from their discriminations without the drug.

It is suggested that, in spite of the cat's possession of a peripheral "color vision" mechanism, the behavioral method employed in the present experiment has produced no evidence of an ability on the part of the animal to respond differentially to lights of different wave lengths which are of equal brightness to the animal.

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Received December 1, 1953.
Early publication.

INFLUENCE OF AMYGDALECTOMY ON SOCIAL BEHAVIOR IN MONKEYS[1]

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Several authors (2, 4, 5) have reported that temporal lobe lesions result in changes in social behavior of monkeys. Since these investigators were only incidentally interested in social behavior, they reported only summary descriptions of their methods or results. It is generally impossible to determine from their reports on what basis they arrived at their conclusions and what, in fact, they meant by social behavior. Therefore, a series of studies using a uniform method of observation has been undertaken to relate brain function to social behavior in monkeys.

Brody and Rosvold (1) reported in detail a method for studying the effects of frontal lobotomy on the social interaction in a colony of *Macaca mulatta*. A similar method was used in the present study of the effects of a temporal lobe lesion on social interaction among monkeys. In addition, the behavior of each monkey, when housed separately, was observed.

METHOD

Animals

Eight young male rhesus monkeys, ranging in weight from 2.90 to 3.85 kg, were housed for a total of 18 two-week periods alternately, either separately in individual cages or together in a large group cage, according to the temporal sequence designated in Table 1. The individual cages were 2 ft. by 2½ ft. by 2½ ft. The group cage was 7½ ft. by 4½ ft. by 6½ ft. and included a movable partition at the center, thus permitting the large cage to be divided into two smaller cages 3¾ ft. by 4½ ft. by 6½ ft. When the monkeys were housed individually, they were fed Rockland monkey pellets and peanuts, one at a time, through the wire mesh of the cage front. When the monkeys were in the group cage, either pellets or peanuts were introduced, one at a time, through a feeding device consisting of a length of 1½-in. pipe mounted obliquely on a stand so as to extend 1 ft. into the large cage. It was fitted at the animals' side with a can containing a small opening large enough to admit only one monkey's paw. At the end of the observation hour, additional pellets were thrown into the group or individual cage, as the situation required, in amounts sufficient to make up the total daily ration of 80 cal/kg body weight per animal. This diet was supplemented three times a week with one-half orange per animal.

Observational: Group Cage

When the animals were together in a group cage, one *E* observed them at the same time each day for 1 hr. during the peanut-feeding situation. Four hours later another *E* observed while introducing the pellets. Food was also frequently offered directly to one or another of the animals, or placed between two monkeys of the group. Diary records were kept of group behavior, and when the typical group interaction had been reliably described, the most dominant—i.e., the highest animal in the hierarchy—was subjected to a two-stage bilateral amygdalectomy. Two other animals were operated on at two-month intervals. During the two weeks allowed for surgery and recovery, all animals were housed individually.

During the latter half of six of the two-week group-cage periods, alterations in group size and living space were instituted to increase interaction and to isolate those parts of the group in which the hierarchy was not clear for more intensive study. In addition, food was withheld from the colony at various times for 48 or 72 hr.

Observational: Individual Cages

At the same time on each day of the individual-cage periods, one *E* observed each monkey while offering it three peanuts. Four hours later, another *E* observed each animal while offering it five pellets. During period 1, diary records were kept of each animal's behavior. At the end of this period, and before placing the animals together for the first time in the group cage, the two *E*s independently ranked the eight animals in order of aggressiveness and/or fearlessness.[2] On each day of succeeding individual-cage periods the monkey's behavior was rated according to the categories listed in Table 2. The total score was used as a measure of the aggressiveness of each animal.

Surgical and Anatomical Procedures

A two-stage myoplastic craniotomy was performed on three of the animals; they were anesthetized with 0.8 cc/kg of a 5 per cent solution of Nembutal injected

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[1] This work was supported in part by grants from Veterans Administration Contracts VAM 23379 and VA 1001-M3222.

[2] Hereafter ratings of individual-cage behavior will be labeled "aggressiveness." They probably could equally as well be labeled "fearlessness." The definition is according to the categories listed in Table 1. In the group-cage situation, however, "aggressiveness" has the objective behavioral referrant of one animal attacking or threatening another.

TABLE 1

Temporal Sequence of Observation Periods

DESCRIPTION	NUMBER (2-wk. periods)	CAGE SITUATION
Preoperative period	1	I
	2*	G
	3	I
	4	G
	5	I
	6	G
1st operation	7	I
1st postoperative period	8*	G
	9	I
	10†	G
2nd operation	11	I
2nd postoperative period	12	G
	13	I
	14*, §	G
3rd operation	15	I
3rd postoperative period	16	G
	17	I
	18*, †	G

Note: *I* refers to individual cage; *G* refers to group cages.

* Large cage divided in two, top four animals in one, bottom four in the other.

† Cage space reduced by one half.

§ Most submissive animal in the group removed from the colony.

TABLE 2

Individual-Cage Behavior Scoring Scheme

CATEGORIES	RATING AND DESCRIPTION
Vocalization	Noisy-loud = +2 Soft noises = +1 Silent = 0
Position at start of of feeding	At front of cage = +3 Goes from front to middle (back) = +2 At middle of cage = +1 At back of cage = 0
Pellet taking	One + for each taken, up to 5. If none taken = 0
Behavior after taking pellets	Stays at front for all pellets = +2 Retreats after each to middle of cage = +1 Retreats after some but not all = +1 Retreats after each to back = 0
Threatening behavior	Jumps at *E* during feeding = +2 Teeth baring or grimacing = +1 Neither = 0
Flight behavior	Animal makes as if to escape = −1 for each time it occurs

Note: Aggressive toward *E* = high positive score (max. +14); fearful of *E* = low positive or negative score.

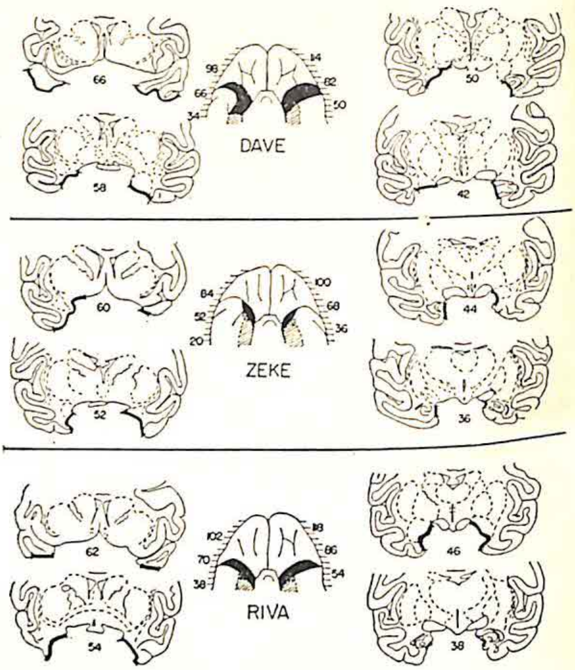

FIG. 1. Representative cross sections and reconstructions of brains of operated animals. Black indicates lesion, xxx indicates spared amygdala, oblique lines indicate spared Ammon's formation.

intraperitoneally. In each case, the left side was operated first and the right side a week later. A semilunar incision was made over the zygoma, curving forward over the orbit. Temporal muscle was split and the zygoma excised. After a burr hole had been enlarged to expose the orbit and temporal fossa, the dura was opened in a cruciate manner. The temporal lobe was retracted, thus exposing the periamygdaloid region just medial and posterior to the Sylvian fissure. An 18-gauge sucker was inserted into the amygdala, and the entire formation removed subpially downward and backward as far as the temporal horn of the ventricle and medially as far as the brain stem. Bleeding was controlled by packing and cautery, and the wound was thoroughly irrigated before closing the dura. Fascia was closed in layers with interrupted silk technique and the scalp with continuous subcuticular stitch.

When the behavioral observations had been completed, the operated animals were sacrificed and their brains prepared for histological examination as described by Pribram and Bagshaw (4).

RESULTS

Anatomical

The reconstruction of the lesions is illustrated in Figure 1. The lesions in the three animals were approximately bilaterally symmetrical. In Dave's brain, in the right hemisphere, the medial portion of the temporal polar cortex, together with all of the amygdaloid complex except for a small portion of the lateral nucleus, was resected. Posteriorly, this lesion invaded the uncal extremity of Ammon's formation. In the left hemisphere, the lesion in the temporal polar cortex was

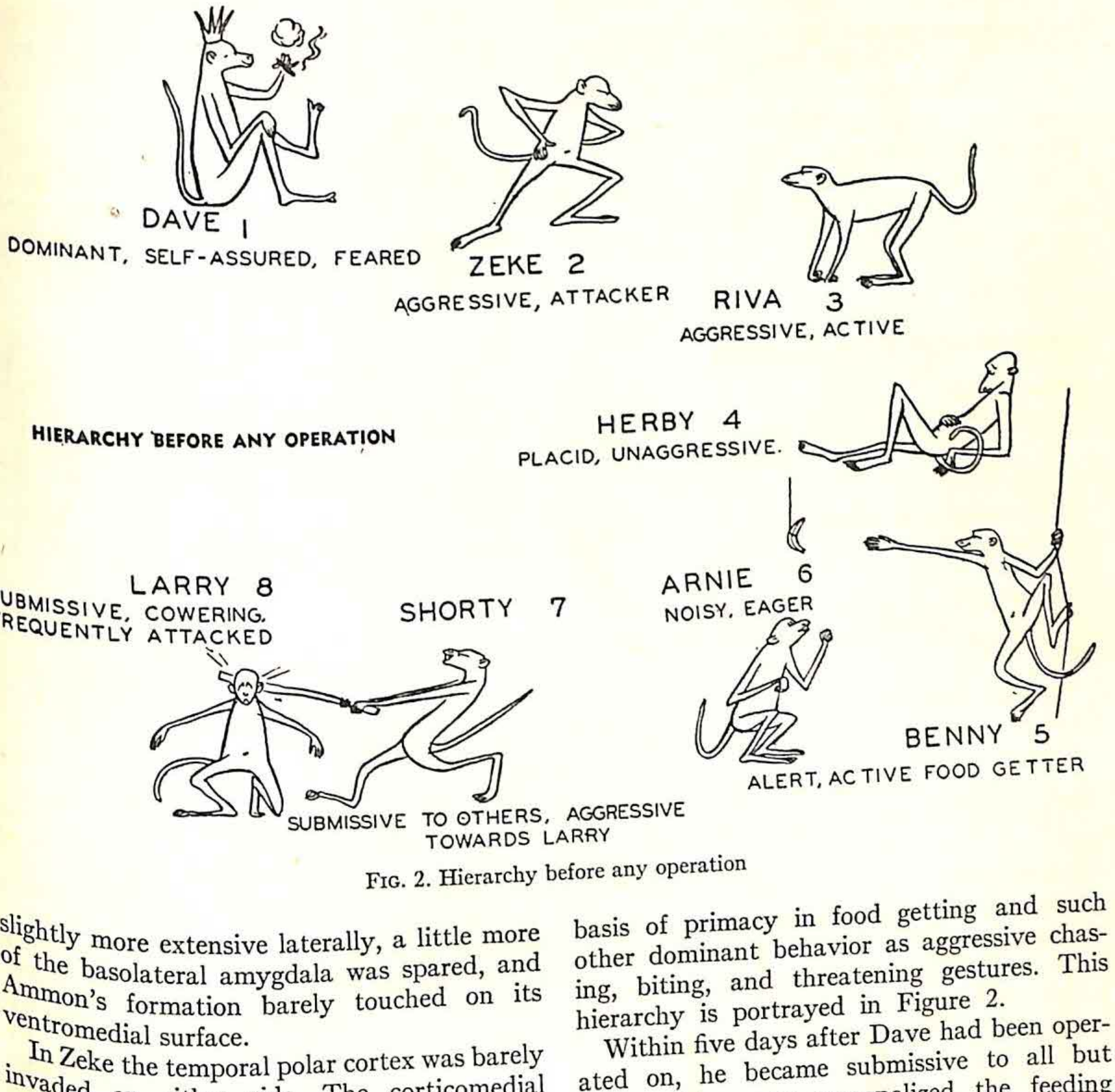

FIG. 2. Hierarchy before any operation

slightly more extensive laterally, a little more of the basolateral amygdala was spared, and Ammon's formation barely touched on its ventromedial surface.

In Zeke the temporal polar cortex was barely invaded on either side. The corticomedial group of amygdaloid nuclei was completely resected bilaterally, but a small portion of the basolateral group remained intact. The posterior end of the lesion barely touched Ammon's formation.

In Riva the lesion invaded the temporal polar cortex bilaterally, and again the corticomedial nuclei of the amygdala were completely resected. However, the basolateral group of nuclei was fairly extensively spared on both sides. The uncal extremity of Ammon's formation was slightly injured on its ventromedial surface.

Group-Cage Behavior

By the second group-cage period a dominance hierarchy was firmly established on the basis of primacy in food getting and such other dominant behavior as aggressive chasing, biting, and threatening gestures. This hierarchy is portrayed in Figure 2.

Within five days after Dave had been operated on, he became submissive to all but Larry. Zeke now monopolized the feeding pipe, dominated the feeding situation, and occupied the preferred floor area of the cage once held by Dave. Toward the end of this period, when the group was divided into top and bottom four, Dave became completely submissive, even to Larry; he avoided other animals, made no attempt to get food, and even refused to accept food from *E*. Attempts to reach Dave's threshold for aggressive response by increasing group interaction were unsuccessful. Even though he would be bitten until blood flowed, he exhibited no aggressive or retaliatory reaction toward the animal that had attacked him.

On the twelfth day after his second operation (the fifth day of group interaction), Zeke

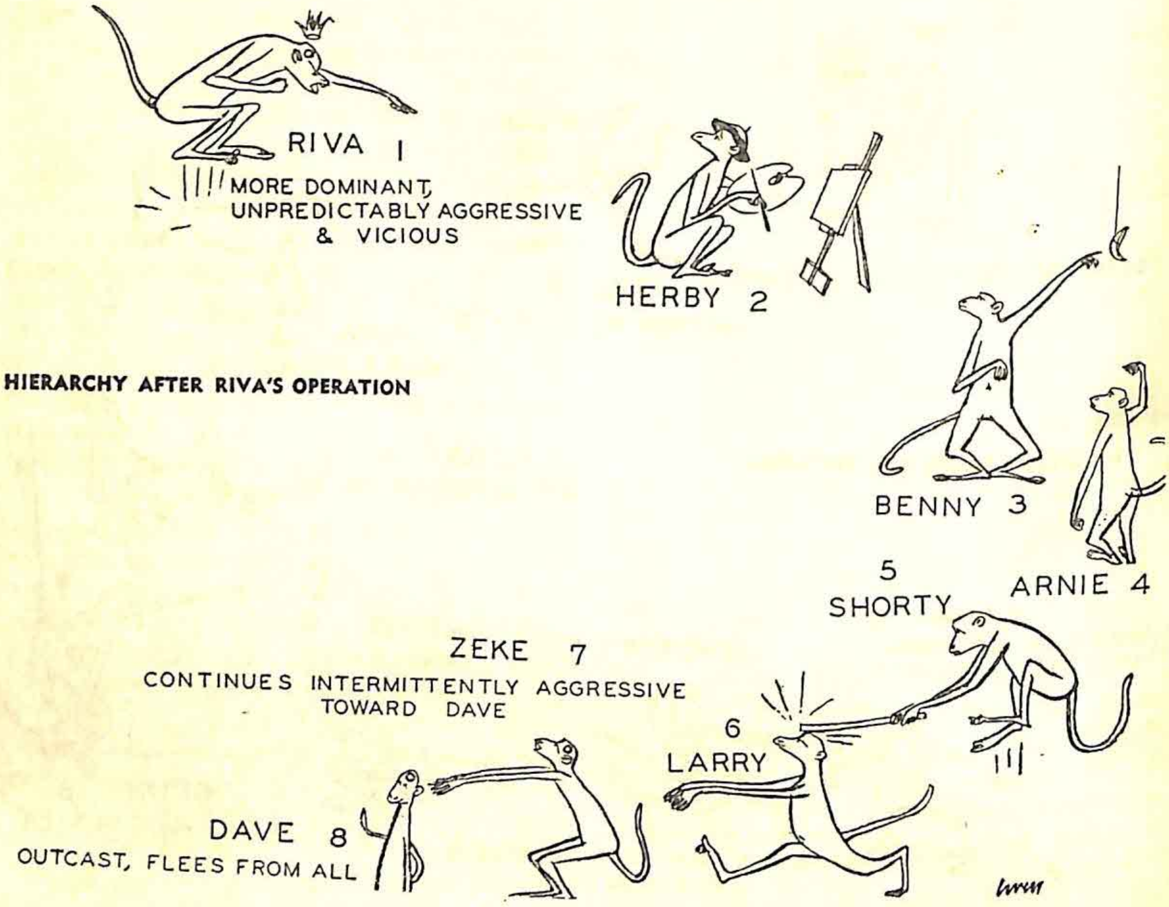
RIVA 1
MORE DOMINANT, UNPREDICTABLY AGGRESSIVE & VICIOUS
HERBY 2
HIERARCHY AFTER RIVA'S OPERATION
BENNY 3
ARNIE 4
5 SHORTY
ZEKE 7
CONTINUES INTERMITTENTLY AGGRESSIVE TOWARD DAVE
6 LARRY
DAVE 8
OUTCAST, FLEES FROM ALL

FIG. 3. Hierarchy after Riva's operation

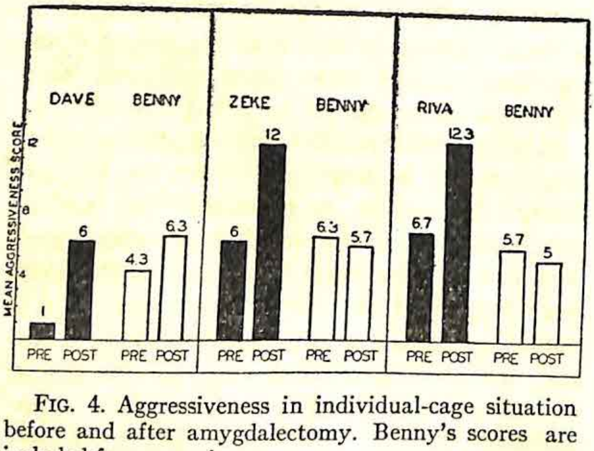

FIG. 4. Aggressiveness in individual-cage situation before and after amygdalectomy. Benny's scores are included for comparison.

became submissive to all but Larry and Dave. Riva now dominated the feeding situation and the food pipe, sharing with no one. Zeke continued to be dominant over Larry and Dave until shortly after the colony was separated into the top and bottom four, when Larry began attacking Zeke. Coincident with this reversal in the Larry-Zeke relationship, Zeke exhibited a tremendous increase in his aggression toward Dave, attacking him almost continuously during the feeding situation. By way of increasing interaction with Zeke, in an attempt to reach his threshold for aggressive response against the other animals in the group, Dave was removed from the colony. This had the effect, *not* of eliciting aggression on Zeke's part, but of eliminating it completely. He now behaved much as did Dave, cringing and fleeing from all, and adopted the tactic of sitting in the corner of the cage and facing the wall.

In contrast to the other two operated animals, Riva did not fall in dominance at any time during the two-month postoperative period. Manipulations of cage space and food deprivation up to 72 hr. were effective only in increasing Riva's aggressiveness. The hierarchy at the end of the experiment is depicted in Figure 3.

Individual-Cage Behavior

The two *E*s agreed significantly better than chance (rho = .95, $p < .01$) on the ranking of the monkeys according to their aggressive behavior in individual cages during the first individual-cage period. This order correlated negatively (rho = $-.595$; $p = .16$) with the hierarchical arrangement that developed in the group cage. In subsequent individual-cage periods, the rating scheme described in Table 1 was used. Figure 4 shows the mean of the last three preoperative and postoperative scores of each animal. The mean scores of a typical nonoperated control, obtained at the same time, are included for comparison. Two months separate the pre- and postoperative measures in each case. A Mann-Whitney (3) *U* test of the significance of the differences in these comparisons indicates that there were no differences in aggressiveness among the monkeys before surgery. Afterward, the scores of the operates show an increase significant beyond the .01 level of confidence, while that of the unoperated animal shows no change.

DISCUSSION

The results of the present study indicate that following amygdalectomy there are marked changes in social behavior of monkeys. However, there are differences among the animals in the direction and degree of this change.

After surgery all operates, though appearing more aggressive in the individual-cage situation, appeared to be less dominant (in two of three cases) in the group-cage situation. In addition to this difference in direction of effect, there is uniformity of change in the individual-cage situation but not in the group-cage situation.

As evident in Figure 2, the differences in direction and degree of change cannot confidently be attributed to differences among the lesions. If variations in extent of damage to the temporal lobe determined the degree of change in behavior, then Dave should have changed most and Zeke least; this was not so either in the group- or individual-cage situation. It is probable, therefore, that one or more of the discrete structures in the temporal lobe are critical in bringing about the alterations in aggressiveness. Since the degree of change in the group-cage situation, i.e., most in Dave and least in Riva, was consistent only with the extent of damage to the basolateral nuclei, these nuclei may be critical for changes in aggressiveness in the group-cage situation.

The differences in direction and degree of change were consistent with the social environment confronting each operated animal after surgery. Upon return to the colony, Dave was confronted with aggressive and active Zeke and Riva; he fell in dominance. Zeke was confronted with Riva; he too fell in dominance. Riva was faced with relatively submissive nonaggressive animals such as Herby; Riva remained dominant.

The differences in direction and degree of change are also consistent with the length of time preoperatively that the dominance-submission relationships had existed. Dave, who changed immediately after his operation, had elicited submissiveness for only six weeks; Zeke, who maintained the No. 1 position for four days after being returned to the colony postoperatively, had elicited submissive responses for 10 weeks; while Riva, who did not change in status, had elicited submissive responses for 16 weeks.

This study, then, suggests that the pattern of social interaction within the group to which it is returned after surgery and the length of preoperative time the relationships had existed may be as important considerations as the locus and extent of a lesion in determining the effects of a brain operation on the social behavior of a monkey. It is meaningless, therefore, to speak of the effect of an operation on "emotional behavior," "social behavior," and the like, without specifying in detail the conditions in which the particular behavior is observed. And, unless the effect of an operation on behavior is studied in a variety of situations, the findings are at best of limited generalizability.

SUMMARY

1. Eight young male rhesus monkeys were studied in individual and group cages for a period of nine months; during this time, the three animals that were most dominant in the group situation were subjected to bilateral amygdalectomy.

2. There was found to be a negative relationship between aggressiveness in the individual-cage and dominance in the group-cage situation before surgery.

3. After amygdalectomy all animals appeared more aggressive in the individual-cage situation. In the group-cage situation, the same animals, in two of three instances, fell from top to bottom positions in the hierarchy. The third animal suffered no loss in dominance and appeared more aggressive in the group situation after operation.

4. The differences in changes in behavior appear to be related to the social environment confronting each animal upon return to the group after surgery and to the length of time the preoperative relationships had existed.

5. The differences in changes in behavior are not related to the differences in extent of lesions as a whole, though they are consistent with differences in damage to the basolateral nuclei of the amygdala.

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Received August 28, 1953.

SUBCORTICAL MECHANISMS IN EMOTIONAL BEHAVIOR: THE EFFECT OF RHINENCEPHALIC INJURY UPON THE ACQUISITION AND RETENTION OF A CONDITIONED AVOIDANCE RESPONSE IN CATS

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The increasing concern in recent years with the role of subcortical mechanisms in emotional behavior has focused considerable attention upon that portion of the rhinencephalon containing the amygdaloid nuclei (7). Durable changes in affective behavior following injury of the amygdala have been reported by several investigators, although agreement as to the specific character of these behavioral alterations is somewhat less than unanimous. Klüver and Bucy (8, 9, 10) reported a diminution of aggressiveness and loss of fear reactions in untamed monkeys after bilateral removal of the temporal cortex and adjacent rhinencephalic structures. However, Spiegel *et al.* (23) observed rage activity in cats immediately after destruction of the amygdaloid nuclei and adjacent structures. Bard and Mountcastle (3), too, report relatively permanent rage and savageness appearing several weeks after placement of similar lesions in cats. More recently, however, Rosvold *et al.* (17), Anand and Brobeck (1, 2), and Schreiner and Kling (19) have failed to find this increased reactivity in dogs, rats, and cats, reporting, rather, a marked docility and friendliness in these preparations following rhinencephalic injury involving the amygdaloid complex.

For the most part, the published reports of these previous investigators have not included data on changes in behavior obtained from the employment of quantitative techniques. In the present study, such techniques have been utilized in an attempt to evaluate more systematically certain aspects of the emotional repertoire of animals sustaining organic deficits of the rhinencephalon. Specifically, this report describes an investigation of the acquisition and retention of a conditioned avoidance response in cats with bilateral surgical lesions largely limited to the amygdaloid nuclei.

METHOD

General Procedure

Twenty-eight adult stock cats, approximately two years old at the start of the experiment, served as *Ss*. The experiment was conducted in two phases: the first investigated acquisition, and the second investigated retention, of a conditioned avoidance response in cats with lesions of the rhinencephalon. In Part I (Acquisition), the 28 cats were divided into three groups, of which 13 animals (groups I and II) were operated prior to conditioning in order to evaluate the effects of the lesions upon acquisition of the avoidance response. Group I (10 experimental animals) sustained bilateral lesions of amygdaloid nuclei *prior* to avoidance training. Group II (three operated control animals) sustained lesions in the hippocampus (two cats) or cingulate cortex (one cat) before avoidance training. Group III (15 unoperated control animals) was trained and used as unoperated controls.

In Part II (Retention), three subgroups were formed from the unoperated control animals of group III in Part I of the experiment to test the effect of the lesions upon retention of a previously learned avoidance response. Subgroup A (three experimental animals) sustained bilateral lesions of the amygdaloid nuclei *following* acquisition of the avoidance response. Subgroup B (three operated control animals) sustained bilateral lesions of the orbitofrontal cortex *following* acquisition of the avoidance response. Subgroup C (three unoperated control animals) acquired the avoidance response and served as controls. All three subgroups were tested for retention of the avoidance response postoperatively. Upon completion of the experiment, the animals were sacrificed, and their brains fixed, sectioned, and stained in order to verify histologically the location of the lesions.

Avoidance Conditioning Procedure

The avoidance response was established in all animals to a 90 per cent criterion by successive daily sets of 30 trials each. All conditioning trials took place in a conventional "double-grill box" with two cubicle chambers (each 24 in. by 24 in. by 16 in.) connected by an open doorway (9 in. by 10½ in). Each chamber consisted of a "grill floor," a heavy glass top and front wall to permit observation and illumination of the chamber, and an earphone attached to the back wall of the chamber for transmission of a clicking noise. Each avoidance conditioning trial consisted of a 30-sec. presentation of a clicking noise (the conditioned stimulus) followed by electric shock (the unconditioned

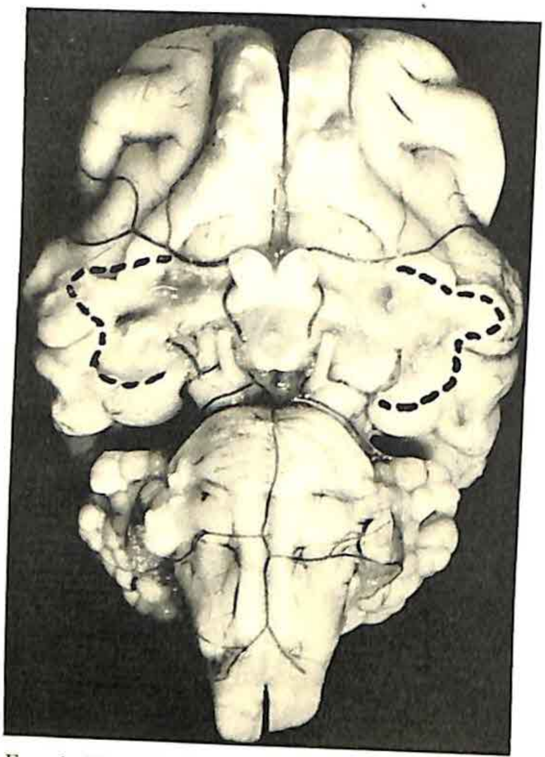


FIG. 1. Ventral view of the brain of a cat with a typical rhinencephalic lesion. The lateral extent of each lesion is indicated by broken lines.

stimulus) through the grill floor of the apparatus. The clicking noise, sounding 16 times per second, was controlled by a switch that operated a synchronous motor and a cam to interrupt the circuit between the secondary coil of a common doorbell transformer and the earphone. Each make and break produced a clicking noise with sufficiently strong high-frequency components to be audible to the cat. A variac in cascade with a power transformer provided an 800-v., 60-cycle current for the grill shock. Tests conducted during actual operation indicated that the current flow varied between 2 and 3 Ma., depending upon the quality of the cat's contact with the grill and *S*'s resistance. Preliminary investigation determined the external resistance, voltage, current, and the like that would make each animal jump and move about, but that, by itself, would not produce violent muscular contractions of a tetanic character. Under the conditions of the experiment, shock magnitude varied around a value of approximately 3.5 Ma., with a range of from 2 Ma. to approximately 6 Ma. in different animals.

The avoidance response consisted of the animal's passage through the open doorway to the opposite side of the box during the 30-sec. conditioned-stimulus interval, thus terminating the clicker and preventing the shock. Failure to make the avoidance response within the 30-sec. conditioned-stimulus interval resulted in onset of the grid shock, which continued until the animal escaped to the opposite side, terminating both clicker and shock. Thirty such conditioning trials were administered during the daily 1-hr. training periods, the interval between each trial being varied randomly between 20 sec. and 5 min. (average intertrial interval, approximately 90 sec.). Spontaneous responses made in the absence of the conditioned clicker stimulus during the intertrial interval were punished by a grill shock of the same magnitude used as the unconditioned stimulus.

In Part I of the experiment (Acquisition), avoidance training was begun several weeks after placement of the lesions. This was deemed advisable in order to insure maximal recovery from the immediate surgical and early postoperative effects, as well as to permit extended observation of gross changes in the animals' behavior independent of any conditioning procedure. Each animal received successive daily sets of 30 training trials until a criterion of 90 per cent conditioned avoidance responses on any single set of 30 trials was reached. In Part II of the experiment (Retention), all animals received 10 sets of daily training trials (300 trials) preoperatively, were operated within a few days after the last set of training trials, and were tested for retention of the responses within two weeks after operation by 5 sets of daily trials (150 trials).

Operative Procedure

All surgery was performed aseptically in one stage under Nembutal anesthesia. In the experimental animals, large bilateral temporal bone flaps were mobilized through an extensive mid-line incision. The dura was incised in an elliptical fashion, bringing into view the entire lateral surface of the temporal lobe and the posterior aspect of the lateral orbitofrontal cortex. With gentle retraction of the temporal lobe, the olfactory stalk, middle cerebral artery, rostral pyriform cortex, and rhinal sulcus were visualized.

Figure 1 shows a ventral view of the brain of a cat with a typical rhinencephalic lesion, the extent of the lesions being indicated by the broken lines. Lesions were made by aspiration. Glass suction tips of appropriate curvature, bore, and design were introduced, and careful aspiration of that part of the pyriform lobes containing the amygdaloid complex was accomplished. The lesions were designed to extend rostrally to the level at which the paleocortex is crossed by the middle cerebral artery. Care was taken to avoid undue manipulation of, or injury to, these vessels. In progressing caudally with the resection, utilizing the rhinal sulcus and its vessels as the lateral boundary, the optic tracts were identified, and all adjacent paleocortical tissue was aspirated. In uncovering the optic tracts, the hippocampal tips were carefully exposed and avoided. This permitted carrying the resection further caudally and medially to ablate the posterior extension of the amygdala and pyriform cortex. After satisfactory homeostasis was obtained, the dura and bone flaps were replaced. Interrupted silk sutures were used to approximate deep tissue layers. The wound edges were opposed, utilizing a continuous silk suture placed in the subcuticular layers of the skin. In those animals sustaining bilateral lesions of the orbitofrontal cortex, the cingulate cortex, and the hippocampus, a similar surgical technique was employed.

In the immediate postoperative period, normal saline and antibiotics were administered parenterally.

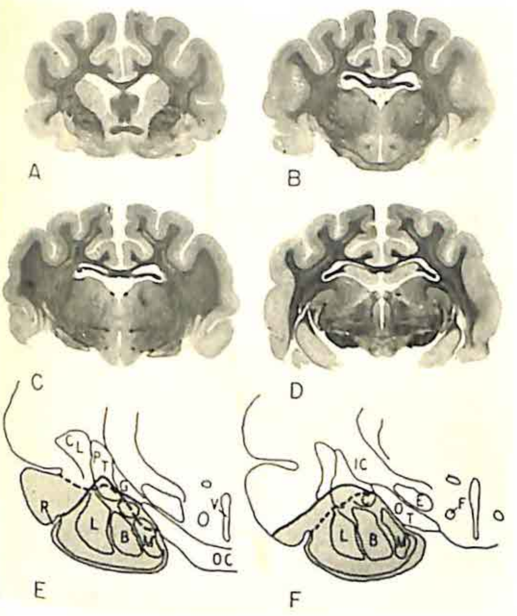


FIG. 2. Photographs of sections taken at various levels through the brain of cat B54 from group I in Part I of the experiment. Section *A*—immediately rostral to the lesions; Sections *B* and *C*—through the greatest extent of the lesions; Section *D*—through the caudal aspect of the lesions. Diagrams *E* and *F* illustrate extent of lesions in Sections *B* and *C*, respectively. Stippled areas below heavy solid lines represent lesions on the left side. Stippled areas below heavy broken lines represent lesions on the right side. Abbreviations are as follows: *B*—basal amygdaloid nuclei, *C*—central amygdaloid nuclei, *CL*—claustrum, *E*—entopeduncular nucleus, *F*—fornix, *G*—globus pallidus, *IC*—internal capsule, *L*—lateral amygdaloid nuclei, *M*—medial amygdaloid nuclei, *OC*—optic chiasm, *OT*—optic tract, *PT*—putamen, *R*—rhinal sulcus, *V*—ventricle.

Until such time as the animals were able to eat and drink voluntarily, they received daily spoon feeding of meat and were given milk via gastric *gavage*.

Histological Procedure

Histological verification of the extent of the lesions was obtained in all operated animals. The brains were fixed in 10 per cent formalin for one to four weeks following removal, and then were cut in serial sections of 50-micra thickness by means of the frozen section technique. Every tenth and eleventh section was mounted, thus providing two parallel series, one of which was stained for cells with thionin, and the other with a modified Weil stain for myelinated fibers. The lesions were reconstructed after observations in both the Weil and thionin series. Figures 2, 3, and 4 show photographic reproductions of sections at various levels through the brains of cats typical of each of the three operated groups.

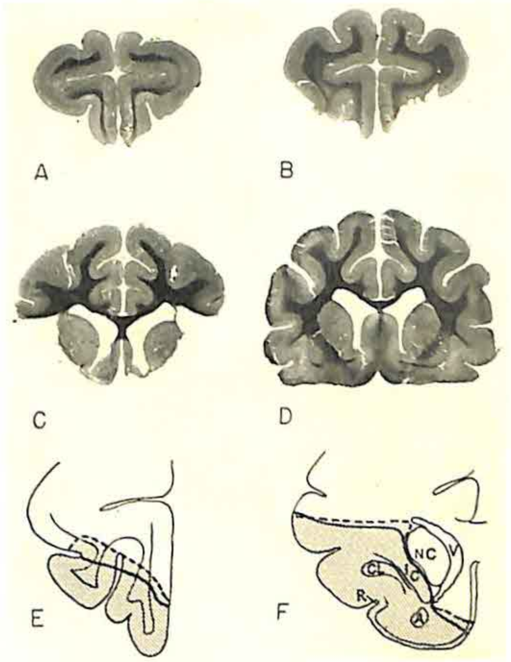


FIG. 3. Photographs of sections taken at various levels through the brain of cat PB2 from subgroup B in Part II of the experiment. Section *A*—immediately rostral to the lesions; Sections *B* and *C*—through the greatest extent of the lesions; Section *D*—through the caudal aspect of the lesions. Diagrams *E* and *F* illustrate extent of lesions in Sections *B* and *C* respectively. Stippled areas below heavy solid lines represent lesions on the left side. Stippled areas below heavy broken lines represent lesions on the right side. Abbreviations are as follows: *A*—anterior commissure, *CL*—claustrum, *IC*—internal capsule, *NC*—caudate nucleus, *R*—rhinal sulcus, *V*—ventricle.

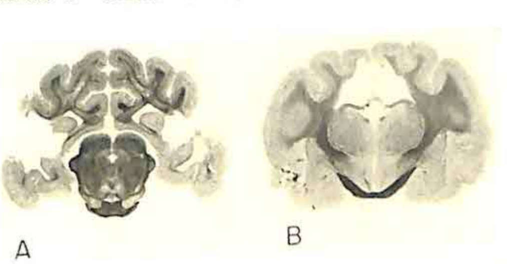
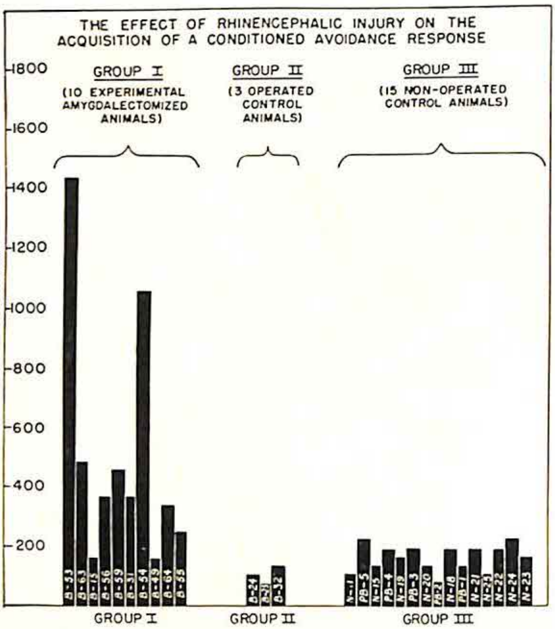


FIG. 4. Photographs of sections taken through the brains of two operated control animals from group II in Part I of the experiment. *A*—photograph taken through the greatest extent of the hippocampal lesion in cat B32. *B*—photograph taken through the greatest extent of the cingulate lesion in cat B24.

RESULTS

General Observations

Each of the 13 experimental animals in Parts I and II of the experiment sustained



[FIG. 5. The effect of rhinencephalic injury on the acquisition of a conditioned avoidance response

extensive bilateral injury of the amygdaloid nuclei and overlying pyriform cortex (Figs. 1 and 2). A more detailed account of the anatomical findings in these preparations, as well as a more extensive description of the behavioral observations made on these cats, has appeared in a previously published report (19). In brief, the salient features of these gross behavioral alterations following rhinencephalic injury may be summarized as follows.

In the immediate postoperative period (first week), the animals appeared lethargic and unresponsive, reacting passively to handling and forced-feeding routines. Within two to three weeks, however, further behavioral changes occurred, which persisted for the duration of the several months' observation and training period. This modified behavior, the salient components of which appeared to be closely interrelated, appearing either simultaneously or in rapid succession, included increased motor activity in response to visual stimuli, exaggerated oral and vocal behavior, relative docility, and a state of marked hypersexuality. None of these changes was observed in either the operated or nonoperated control animals. A cinematographic record was prepared in conjunction with these experiments to illustrate the character of these gross behavioral changes following paleocortical injury (18).

Each of the three operated control animals in Part II of the experiment sustained bilateral extirpation of the rostroventral aspects of the cerebral hemispheres (Fig. 3). The extent of the injury in these preparations included the orbital and proreus gyri, together with the rostral rhinencephalon, adjacent portions of the claustrum, anterior commissure, and a large ventral part of the internal capsule of each side. Since the corticipetal outflow of the thalamic dorsomedial nucleus is transmitted through this obliterated segment of the internal capsule (5, 15), it appears likely that any remaining cortical projection field of this nucleus was functionally isolated. Cortical regions lateral and posterior to the area of termination of the dorsomedial nuclei were included in the lesions of this control group because of previously reported decrements in learning and retention following such injury in experimental animals (7).

Effects on the Acquisition of the Conditioned Avoidance Response

Figure 5 shows the number of trials required for each of the 28 animals in Part I to reach the 90 per cent conditioned avoidance criterion. By training trial 210, all 18 operated and nonoperated control animals (groups II and III) had acquired the avoidance response to the criterion level. Only two of the ten experimental animals (group I), however, had reached the 90 per cent criterion level by trial 210. This difference in rate of acquisition of the conditioned avoidance response between the experimental amygdalectomized animals (group I) on the one hand, and the operated and nonoperated control animals (groups II and III) on the other, is highly significant by Fisher's (6) exact 2 × 2 test ($p < .01$). Rhinencephalic injury appears to have markedly impaired acquisition of the avoidance response in the experimental animals.

Gross behavioral observations made during the course of avoidance conditioning in Part I of the experiment revealed other rather striking differences between the experimental amygdalectomized cats and both the operated and nonoperated control animals. The normal control cats, in the early stages of avoidance learning, evidenced considerable "emotional" behavior associated with the onset of the conditioned stimulus. Defecation, urination, vocalization, and piloerection almost inevitably occurred during the conditioned stimulus interval after the first few conditioning trials prior to the animals' learning the avoidance response. As the conditioned avoidance response increased in frequency, however, these autonomic accompaniments of the animals' reaction to the conditioned stimulus invariably faded from the picture. It is striking that such reactions to the conditioned clicker stimulus were rarely, if ever, observed in the experimental amygdalectomized animals operated prior to avoidance training, although none of these preparations showed any impairment of the unconditioned escape response to the shock stimulus.

Effects on the Retention of the Conditioned Avoidance Response

Figure 6 shows the mean percentage of conditioned responses for the experimental (subgroup A), operated control (subgroup B), and nonoperated control animals (subgroup C) on both the pre- and postoperative sets of avoidance trials in Part II of the experiment. No significant difference between the three groups appears on the 300 preoperative acquisition trials. Furthermore, neither the experimental amygdalectomized (subgroup A) nor the unoperated control animals (subgroup C) showed any significant decrement in retention of the avoidance response on the 150 postoperative trials. The operated control animals (subgroup B), however, which sustained bilateral lesions of the orbitofrontal cortex (Fig. 3), failed either to retain or relearn the avoidance response postoperatively. None of these latter preparations made a single conditioned avoidance response during the first 150 postoperative trials. The difference between the mean percentage of conditioned avoidance responses on the last 30 preoperative trials and the first 30 postoperative trials for the operated control frontal lobectomized animals (subgroup B) is highly significant ($p < .01$). In addition, the difference between the mean percentage of conditioned avoidance responses on the first 30 postoperative trials for the operated control frontal animals (subgroup B) and both the experimental amygdalectomized animals (subgroup A) and the nonoperated control animals (subgroup C) is also highly significant ($p < .01$).

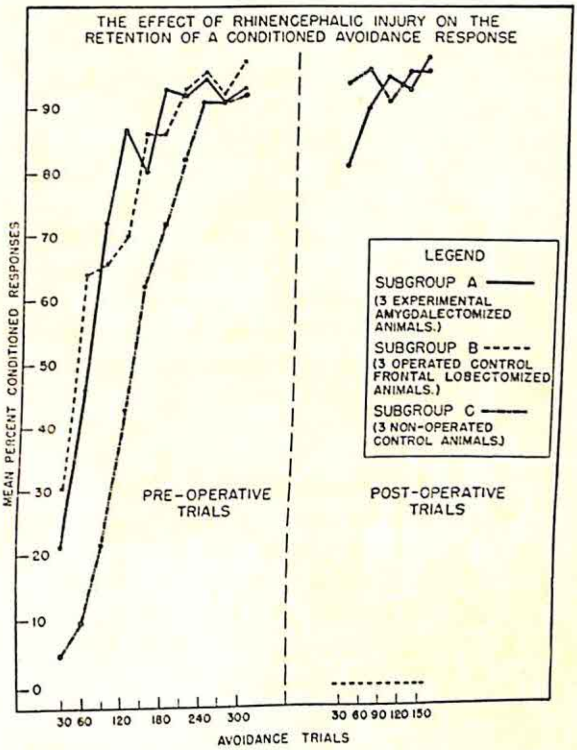


FIG. 6. The effect of rhinencephalic injury on the retention of a conditioned avoidance response

Cat PB3 has been included in both subgroup A and subgroup B, having initially sustained bilateral amygdalectomy without effect upon the avoidance response and then subsequently sustaining the orbitofrontal lesions. Although the difficulties inherent in the inclusion of this animal in both groups, for purposes of statistical treatment of the results, are quite apparent, the marked contrast between the effects of amygdala and those of frontal lesions upon retention of the avoidance response is brought out in sharp relief by this two-stage operative procedure.

The postoperative behavior of the operated control cats with orbitofrontal lesions during retraining trials for the conditioned avoidance response in this part of the experiment also provided a rather striking contrast to the previously discussed reactions of the amygdalectomized animals in Part I of the experiment. Like the normal control animals, these orbitofrontal preparations evidenced considerable autonomic disturbance in their responses to presentation of the conditioned stimulus in the early stages of the conditioning procedure. Indeed, defecation, urination, piloerection, and vocalization in response to presentation of the conditioned stimulus continued to appear throughout the course of the 150 postoperative retraining trials given these animals, and unconditioned escape responses to the shock stimulus were elicited on each trial. Figure 6 indicates quite clearly, however, that not a single avoidance response was recorded throughout this period.

DISCUSSION

The results of these experiments indicate quite clearly that rhinencephalic injury in the cat, largely restricted to the amygdaloid nuclei, can affect differentially the acquisition and retention of a conditioned avoidance response. The experimental amygdalectomized animals (group I) operated prior to avoidance training in Part I of the experiment showed a significant impairment in the rate of acquisition of the avoidance response that was not apparent in either operated (group II) or nonoperated control animals (group III). The experimental amygdalectomized animals (subgroup A) operated following avoidance training in Part II of the experiment, however, showed no deficit in retention of the avoidance response. These findings, plus the fact that the amygdalectomized animals in Part I of the experiment did ultimately learn the avoidance response, if somewhat more slowly, suggest that the amygdaloid nuclei may play a facilitative role in the acquisition of such an avoidance response, but that these nuclei do not appear to constitute a necessary condition for either acquisition or retention of such avoidance behavior.

This facilitative function of the amygdaloid nuclei in the acquisition of a conditioned avoidance response suggests interesting implications for theoretical formulations of avoidance *learning* when considered in the light of more recent efforts to define the role of the rhinencephalon and the "visceral brain" in affective expression (11, 16). The "anxiety" or "fear-reduction" hypothesis, currently associated with theoretical accounts of the *acquisition* of avoidance responses (12, 14), could be expected to find some support in the results of these experiments, *if* the assumption of a correlation between the neural structures injured in these experiments and emotional expressions of "fear" or "anxiety" is justified. Indeed, such an extrapolation of the present data appears quite consistent with previously reported observations on the same animals (19). Schreiner and Kling report that these same preparations "failed to exhibit fear, escape activity, or normal defensive and aggressive behavior when placed in unrestricted association with unfriendly animals of other species (mice, agoutis, dogs, and monkeys)" (p. 648). Further, these authors state that the amygdalectomized animals "displayed elevated thresholds for the elicitation of anger" (p. 648). Then, too, the observation reported above, relative to the rather marked deficit in autonomic responsivity found in the amygdalectomized animals in the absence of any impairment of the unconditioned escape response during the course of avoidance conditioning, is consistent with such a formulation. It might be predicted from the "fear-reduction" hypothesis relative to the motivational aspects of avoidance learning that such animals, deprived of normal affective functioning, would show some impairment in avoidance learning.

Experiments conducted by Solomon and Wynne (21) during the past few years, investigating avoidance conditioning in dogs with deficient autonomic functioning as a result of surgical and pharmacological sympathectomy, provide corroborative data on the role of the presumed neural correlates of "fear" and "anxiety" in avoidance behavior. These authors report a similar impairment of avoidance learning following sympathectomy in their experimental animals. Recent formulations of the relationship of the "visceral brain" (including the amygdaloid nuclei) to autonomic function (11) make the relevance of these latter findings to the present data, and to theoretical formulations of avoidance learning, obvious.

The viewpoint that "fear" or "anxiety reduction" plays a central motivational role in the *maintenance* or *retention* of avoidance behavior once the response has been acquired (4, 14), however, will find little support in the results of the present experiments. If injury of the amygdaloid nuclei produces some deficiency in the animals' ability to demonstrate "fear" or "anxiety"—as indeed the results of this and previous experiments (18, 19) seem to indicate—then the results obtained in Part II of the experiment, indicating that no impairment of retention of the avoidance response follows the production of such lesions, would appear to be inconsistent with the hypothesis that "fear reduction" plays a central motivational role in the *maintenance* of avoidance behavior. A more plausible formulation of the avoidance-conditioning situation, consistent with the present findings as well as with previously reported observations of such animals with rhinencephalic injury and other autonomic deficiencies, would visualize the *acquisition* and *maintenance* of avoidance behavior from the viewpoint of a *two-process* learning theory (13, 20, 22). Indeed, the present findings suggest quite strongly that both classical or respondent conditioning and instrumental or operant conditioning may play a role in avoidance learning under normal circumstances, with classical conditioning providing at least a facilitative, if not necessary, condition.

Within the framework of such a two-factor formulation of the avoidance-conditioning process, the results obtained with the operated control frontal lobectomized animals (subgroup B) in Part II of the experiment may provide some suggestion relevant to the neural correlate for the instrumental or operant aspects of avoidance behavior. It is clear that animals with such lesions show virtually a complete loss of the previously conditioned avoidance response after operation. The conditions under which such animals may relearn and retain such a response are not as yet clear from these data, however, although experiments are presently in progress to explore this parameter.

SUMMARY

The present report describes an experiment investigating the acquisition and retention of a conditioned avoidance response in cats with surgical lesions largely limited to the amygdaloid nuclei. The avoidance response consisted of the cat's passage through an open doorway separating the two compartments of a conventional "double-grill" box in response to the presentation of a 30-sec. conditioned clicker stimulus, thus terminating the clicker and preventing the shock which followed the failure to respond within the 30-sec. interval.

1. In Part I of the experiment (Acquisition) 28 adult stock cats were divided into three groups. Group I (ten animals) sustained bilateral lesions of the amygdaloid complex prior to avoidance training. Group II (three animals) sustained lesions in the hippocampus (two cats) or cingulate cortex (one cat) prior to avoidance training. Group III (15 animals) was trained, and served as unoperated controls. The avoidance response was established in all animals to a 90 per cent criterion by successive daily postoperative sets of 30 trials each. The amygdalectomized animals (group I) required significantly more training trials to reach criterion than either the operated (group II) or unoperated (group III) control animals.

2. In Part II of the experiment (Retention), three subgroups were formed from the unoperated control animals (group III) of Part I of the experiment. Subgroup A (three animals) sustained bilateral lesions of the amygdaloid nuclei, and subgroup B (three animals) was subjected to bilateral lesions of the orbitofrontal cortex *following* acquisition of the avoidance response. Subgroup C (three animals) served as unoperated controls. Postoperative tests in all three subgroups revealed no significant decrement in retention of the avoidance response in either the amygdalectomized cats (subgroup A) or the unoperated control cats (subgroup C). In contrast, cats with lesions of the orbitofrontal cortex (subgroup B) showed no retention of the avoidance response even after 150 retraining trials.

3. Upon completion of the experiments, the animals were sacrificed, and the lesions reconstructed histologically.

4. The implications of these findings for theoretical formulations of avoidance learning have been discussed.

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Received August 3, 1953.

VISUAL DISCRIMINATION PERFORMANCE FOLLOWING PARTIAL ABLATIONS OF THE TEMPORAL LOBE: II. VENTRAL SURFACE VS. HIPPOCAMPUS[1]

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This study is the second in a series dealing with the effects of partial ablations of the temporal lobes on visual discrimination performance. Results of the initial experiment (5) demonstrated that marked impairment on visual discriminations may be produced by lesions limited to the ventral portions, including the hippocampal formation and the cortex on the ventral surface, as compared with lesions of the lateral portions of the lobe. The present investigation was designed to delimit further the locus and extent of damage necessary to produce gross decrement in performance. To this end, comparisons were made of the effects of separate ablations of ventral temporal cortex and of the hippocampal formation.

An additional aim of the experiment was to determine whether or not the occurrence and degree of deficit vary directly as a function of test difficulty. Evidence suggesting such a relationship was presented in the earlier study; however, the results were not conclusive since the postoperative deficits appeared to be related also to the particular sequence in which the tests were administered. In the present experiment, therefore, the sequence of presentation was controlled, in order to permit an evaluation of the effects of test difficulty per se.

METHOD

Subjects

Eight immature male monkeys (*Macaca mulatta*), ranging in weight from 3 to 7 kg., were divided into three operate groups and subdivided into two training groups.

Surgical Procedures

Animals were anesthetized with sodium amytal (0.6 cc. per kg. body weight) injected intraperitoneally. The temporal bone was removed and the dura incised over the lateral surface of the temporal lobe. For those animals that were to receive ablations of the anterior portions of the lobe, the zygoma was removed in order to expose the pole; for all other operates anastomotic veins were coagulated and severed at their entrance into the lateral sinus to permit exposure of the ventral surface. Cortex was removed by subpial aspiration with a small-gauge sucker. Symmetrical bilateral operations were performed in two stages, left hemisphere first, with two to three weeks separating the unilateral removals.

Ventral surface lesions. An attempt was made to resect the inferior temporal, fusiform, and posterior hippocampal gyri in animals VT-1,-2, and-3.

Hippocampectomies. Resection of the hippocampal formation was attempted through an incision in the inferior convolution in animals H-1 and H-2, and via the amygdaloid complex in animal HA.

Control lesions. Resections that controlled for the incidental damage associated with the hippocampectomy procedures were performed on animals HC and HAC. In HC, the control for H-1 and H-2, a scalpel incision was made in the inferior convolution and extended into the temporal horn of the lateral ventricle; but the hippocampal formation itself, visible in the floor of the ventricle, was not resected. In HAC, the control for HA, the periamygdaloid cortex and amygdala were resected, but the hippocampal formation, visible posteriorly, was left intact. In order to control also for extent of lesion in the H and VT operates, the resection in HAC was extended to include the lateral polar cortex and the superior temporal convolution including the supratemporal plane.

Tests

Tests included the direct method of delayed response with a sliding panel interposed during delay, and five visual discriminations, the paired discriminanda consisting of: (*a*) an inverted and an erect equilateral triangle, each with an area of 2 sq. in. and painted flat black on yellow backgrounds; (*b*) a cut-out circle and a cut-out square, both of wood ½ in. in height and 4 sq. in. in top surface area, painted flat black and mounted on yellow backgrounds; (*c*) four horizontal stripes and a diamond, each covering an area of 3 sq. in., painted flat black on white backgrounds; (*d*) red (RT-1) and green (GT-1) Color-Aid papers (Color-Aid

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[1] Supported in part by a grant from Contract VAm-23379 of the Veterans Administration to Dr. John F. Fulton. This report covers material contained in a thesis submitted to McGill University, 1951, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author wishes to express his appreciation to Drs. K. H. Pribram, H. E. Rosvold, and D. O. Hebb for their assistance and advice on various phases of the study, to Miss Lila Rupp for the histological preparation of the brains, and to Mrs. Marilyn Tucker for help with the preparation of the manuscript.

Company, New York, N. Y.); and (*e*) light gray (Gray 3) and dark gray (Gray 6) Color-Aid papers.

Preoperatively, animals were trained on delayed response at 0-, 5-, and 10-sec. delays presented in succession; postoperatively, only the 10-sec. interval was used.

On the first discrimination, the inverted triangle was the rewarded stimulus for all animals. On the last four discriminations, however, the first stimulus of each pair was made positive for four of the animals (VT-2, H-1, H-2, HC) and negative for the other four. This procedure was adopted to determine whether or not the rapid preoperative learning of these tasks in the previous study (5), in which the rewarded stimuli were the same for all animals, could have been due to an initial preference for the positive discriminanda.

The experiments were conducted in an air-conditioned, soundproof room. The testing cage faced a sliding panel which, when raised, disclosed two rectangular cups spaced 12 in. apart. Each cup was covered by a 3-in. by 4-in. plaque—unpainted for delayed response, painted as background for the black patterns, and entirely covered by the papers—which the animals learned to displace to obtain the concealed reward. A one-way–vision screen separated the animal from *E*. Daily testing sessions consisted of 30 trials a day with left and right cups baited in a predetermined balanced order. The noncorrection technique was employed, and no punishment, other than withholding the peanut reward, was given for errors.

In addition to the delayed response and visual discrimination tasks, other procedures were used for evaluating changes in extent of visual field, visual acuity, and reactions to food vs. nonfood and aversive vs. indifferent stimuli. These informal tests, involving no special training, have been described by Chow (3) and were outlined in the previous paper of this series.

Training Schedule

Preoperatively, all animals were trained to a criterion of 90 correct in 100 consecutive trials on delayed response, inverted-erect triangle, circle-square, stripes-diamond, red-green, and light gray–dark gray, in succession. Two weeks postoperatively, this order of presentation was maintained the *same* for four animals—VT-2, VT-3, H-2, and HA—and *reversed* for four—VT-1, H-1, HC, and HAC. The two training groups will be designated group S and group R, respectively.

Determinations of extent of visual field, visual acuity, and reactions to inedible and aversive objects were made in one daily session before operation. These tests were then repeated once after the unilateral removals, once within the first two weeks following the contralateral removals, and at semimonthly intervals thereafter.

Anatomical Procedures

Upon completion of the behavioral observations, the animals were sacrificed, their brains imbedded in celloidin, and the blocks serially sectioned at 25 mμ. Every twentieth section was stained with aniline thionin and every fourth stained section was used to reconstruct the lesions. The thalami, as well as the structures surrounding the ablation, were examined microscopically for evidence of damage or degeneration.

Reconstructions of the lesions and representative cross sections are presented in Figure 1. The operative results on two animals, HC and H-2, show considerable deviation from the intended removals. In both cases, in addition to deep incisions through the inferior convolution, large portions of ventral cortex are ablated bilaterally; and in HC, the lateral cortex of the left hemisphere is extensively damaged, apparently as a result of postoperative dural adhesions. The resections performed on the six other animals, however, conform in general to the experimental plan. Relatively minor deviations may be noted: slight damage to the posterior portion of the hippocampal formation in the left hemisphere of VT-1 (see Table 1); bilateral sparing of the posterior portion of the hippocampal gyrus in VT-2; invasion of ventral occipital cortex bilaterally in VT-2 and in the right hemisphere of VT-3; ablation of the right hippocampal gyrus but sparing of the posterior portion of the left hippocampal formation in HA; and incomplete destruction of the amygdaloid complex in HAC.

Retrograde thalamic degeneration findings are given in Table 1. Whereas the extensive bilateral involvement of the lateral geniculate bodies in H-2 is due in part to direct damage, gliosis and fading of cells in the ventrolateral horn, found also in VT-3 and HC, appear to be the result of damage to the ventral portion of the optic radiations. Degeneration in the medial geniculate bodies is present only in HAC, the one operate with a lesion of the supratemporal plane. In contrast to these isolated instances of geniculate involvement, pulvinar degeneration is found in all animals. The six operates with ventral surface damage or with incisions through the inferior convolution VT-1, -2, -3; H-1, -2; and HC, have degeneration in the posteroventral portion of *n. pulvinaris lateralis*; and the majority of these animals have degeneration also in the ventral portion of *n. pulvinaris inferior*. In the two remaining operates, HA and HAC, the posterior tip of *n. pulvinaris medialis* is involved, probably as a result of lateral polar resections (2). These findings of retrograde degeneration agree in detail with those reported for baboons (5).

RESULTS

Informal Tests

Transient visual field defects opposite the side of lesion were found in HC and H-2 following the unilateral operation, and again in H-2 after the contralateral operation. Animal H-2's transient partial anopsia may account for the indiscriminate examination of food and nonfood that it exhibited for nearly two months following the second removal. No other operates showed visual field or acuity changes, or failure on the food-nonfood discrimination.

The two animals with ablations of the pole

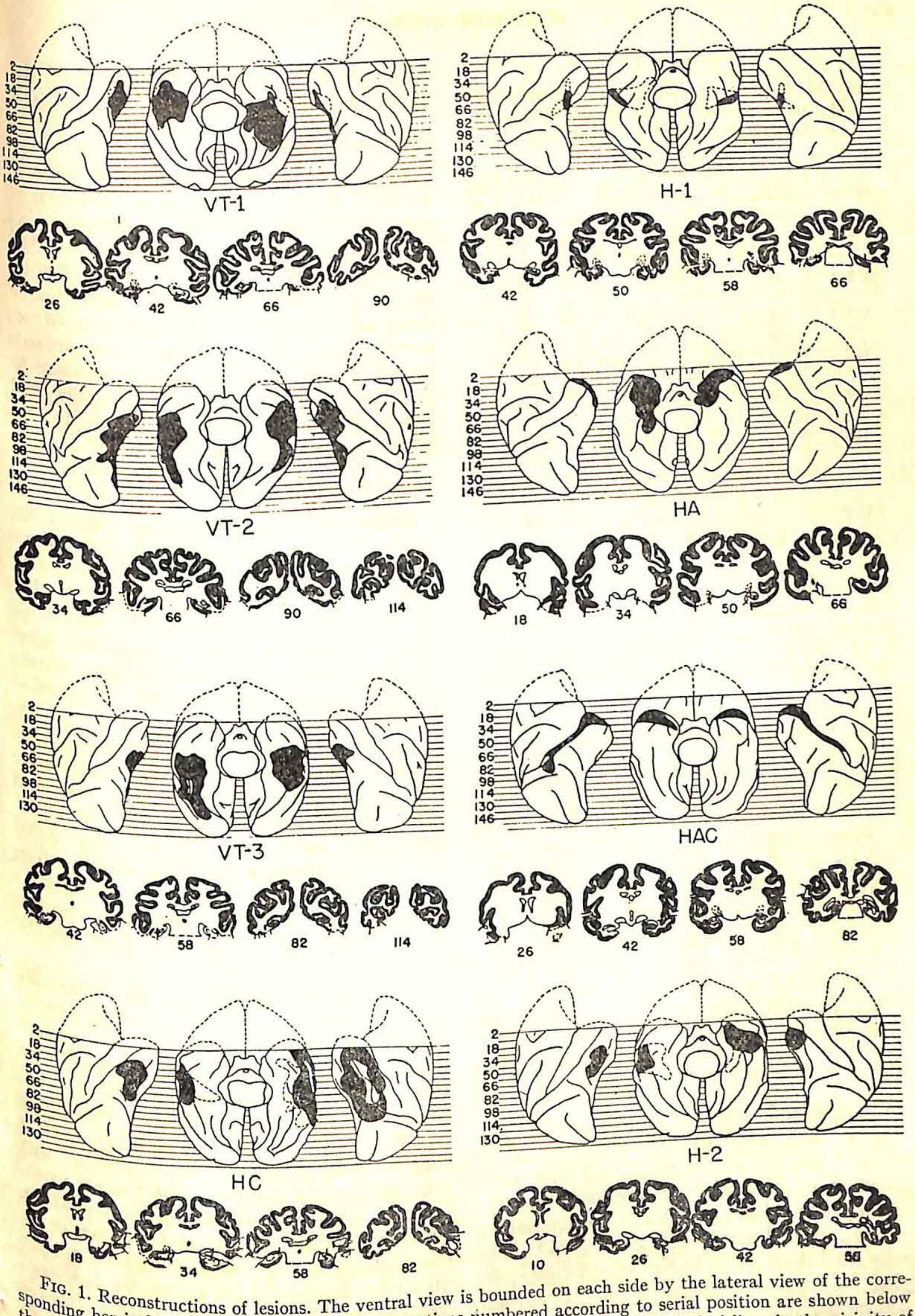

FIG. 1. Reconstructions of lesions. The ventral view is bounded on each side by the lateral view of the corresponding hemisphere. Four representative cross sections numbered according to serial position are shown below the reconstructions for each animal. In the reconstructions black indicates lesion; dashed lines in the vicinity of lesion indicate deep damage. In the sections black indicates intact cortex.

TABLE 1

Extent of Damage to Amygdaloid Complex and Hippocampus and Extent of Retrograde Degeneration in Geniculate Bodies and Pulvinar

ANIMAL	HEMI-SPHERE	AC	HF	LG a	MG p	PL pv	PI v	PM pv
VT-1	rt.	—	—	—	—	S	—	—
	lt.	—	L	—	—	?	—	—
VT-2	rt.	—	—	—	—	S	?	—
	lt.	—	—	—	—	S	—	—
VT-3	rt.	—	—	S	—	S	L	—
	lt.	—	—	S	—	S	S	—
H-l	rt.	?	C	—	—	S	?	—
	lt.	—	C	—	—	?	S	—
HA	rt.	C	C	—	—	—	—	S
	lt.	C	S	—	—	—	—	S
HAC	rt.	L	—	—	S	—	—	S
	lt.	L	—	—	S	—	—	?
HC	rt.	—	?	S	—	L	?	—
	lt.	—	—	L	—	S	S	—
H-2	rt.	—	C	C	—	L	L	—
	lt.	?	C	L	—	L	S	—

Note: *AC*, amygdaloid complex; *HF*, hippocampal formation; *LG*, lateral geniculate bodies; *MG*, medial geniculate bodies; *PL*, *n. pulvinaris lateralis; PI*, *n. pulvinaris inferior; PM*, *n. pulvinaris medialis; a*, anterior; *p*, posterior; *pv*, posteroventral; *v*, ventral. Extent of damage and of degeneration is indicated as follows: *C*, almost complete; *L*, large; *S*, small; *?*, small doubtful; —, none.

TABLE 2

Visual Spatial Delayed Response

ANIMAL	GROUP	PREOPERATIVE		POSTOPERATIVE	
		Trials	Errors	Trials	Errors
VT-1	R	290	69	20	5
VT-2	S	130	32	0	0
VT-3	S	740	240	330	68
H-1	R	350	85	50	11
HA	S	170	40	140	47
HAC	R	200	57	50	24
HC	R	210	60	0	0
H-2	S	200	57	50	24

Note: Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. Preoperative trials and errors at 0-, 5-, and 10-sec. delays are combined into one total score, whereas postoperative trials and errors are for the 10-sec. delay.

and amygdaloid complex showed gross alterations in their responses to previously aversive stimuli. Trainer's gloves and net not only failed to evoke avoidance reactions, but frequently elicited manual and oral examination instead. The behavior of animal HAC, in which the destruction of the amygdaloid complex was incomplete, reverted to normal within the first few postoperative weeks; in animal HA, however, these behavioral alterations persisted until it was sacrificed five months after operation.

Delayed Response

Results for delayed response are given in Table 2. Retention tests were conducted at only the 10-sec. interval; nevertheless, all eight operates attained criterion in less than the total number of trials and errors they required preoperatively. Whereas there was no consistent relationship between rate of relearning and locus of lesion, the animals (group R) that received delayed response as the last postoperative test generally had greater saving than those (group S) that received delayed response first.

Visual Discriminations

Lesions. Results for the three pattern discriminations are shown in Table 3 and those for the red-green and light gray–dark gray discriminations are given in Table 4. The scores obtained by HC and H-2 cannot be used for the evaluation of the effects of selective damage since both animals had unintentionally extensive ablations (see *Anatomical Procedures*). Rated in terms of degree of impairment (measured as the absolute difference between postoperative and preoperative scores), these two operates rank first and third, respectively, in the series of eight. Both failed to relearn or were retarded by 600 trials in relearning each of the three pattern discriminations. In addition, operate H-2 showed a 400 to 500 trial deficit on the differential reactions to red and green and to light gray and dark gray.

Comparisons among the six remaining animals indicate that the three with ventral surface ablations (VT-1, -2, and -3) showed greater impairment than the three with lesions elsewhere in the temporal lobes (H-1, HA, and HAC). Thus, within training group R, animal VT-1 failed both the inverted-erect triangle and circle-square discriminations and was retarded by more than 600 trials in relearning the stripes-diamond discrimination. Operates H-1 and HAC, on the other hand, relearned these tasks with deficits no greater than 150 trials, and in the case of the inverted-erect triangle discrimination, with savings in terms of errors. Similarly, in training group S, VT-2 failed in 1,000 trials and VT-3 required

TABLE 3

Visual Discriminations: Patterns

ANIMAL	GROUP	INVERTED TRIANGLE–ERECT TRIANGLE				CIRCLE–SQUARE				STRIPES–DIAMOND			
		Pre		Post		Pre		Post		Pre		Post	
		T	E	T	E	T	E	T	E	T	E	T	E
VT-1	R	240	(89)	1000	(399)	150	(79)	1000	(398)	80	(26)	740	(53)
VT-2	S	200	(100)	1000	(502)	60	(20)	370	(106)	10	(9)	0	(0)
VT-3	S	200	(104)	890	(368)	200	(97)	370	(112)	0	(0)	10	(5)
H-1	R	210	(98)	220	(49)	50	(16)	200	(42)	10	(6)	140	(44)
HA	S	350	(146)	240	(54)	180	(74)	40	(4)	0	(0)	0	(0)
HAC	R	160	(76)	170	(40)	150	(69)	220	(87)	80	(35)	110	(54)
HC	R	270	(122)	1000	(253)	80	(21)	680	(228)	0	(0)	540	(219)
H-2	S	560	(259)	1000	(492)	100	(44)	1000	(456)	20	(12)	1000	(475)

Note: Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. A score of 1000 trials denotes failure to attain the criterion within the limits of training. *Pre* = preoperative; *Post* = postoperative; *T* = trials; *E* = errors (in parentheses).

TABLE 4

Visual Discriminations: Hue and Shades of Gray

ANIMAL	GROUP	RED-GREEN				LIGHT GRAY–DARK GRAY			
		Pre		Post		Pre		Post	
		T	E	T	E	T	E	T	E
VT-1	R	0	(0)	0	(0)	30	(27)	10	(4)
VT-2	S	0	(0)	0	(0)	0	(0)	0	(0)
VT-3	S	0	(0)	0	(0)	10	(4)	0	(0)
H-1	R	0	(0)	0	(0)	0	(0)	0	(0)
HA	S	0	(0)	0	(0)	0	(0)	0	(0)
HAC	R	0	(0)	0	(0)	10	(5)	0	(0)
HC	R	0	(0)	0	(0)	20	(14)	0	(0)
H-2	S	0	(0)	530	(258)	0	(0)	400	(171)

Note: Scores are trials and errors preceding 90 correct choices in 100 consecutive trials. *Pre* = preoperative; *Post* = postoperative; *T* = trials; *E* = errors (in parentheses).

almost 900 trials to relearn the inverted-erect triangle discrimination; both were retarded by 200 to 300 trials in relearning the differential reactions to circle and square; in contrast, HA attained criterion on these tasks with savings of more than 100 trials over its preoperative scores.

Sequence of presentation. Analysis of the effects of differences in postoperative training procedures shows that reversing the preoperative order of presentation resulted consistently in greater impairment on tasks intermediate in the sequence (circle-square, stripes-diamond) than did maintaining the preoperative order. Thus, among the ventral-temporal operates, the animal in group R (VT-1) failed completely to relearn the pattern discrimination that both group S animals (VT-2, VT-3) relearned with deficits; and it was severely retarded in relearning the pattern discrimination that both group S animals retained. Similarly, among the three operates without ventral-temporal ablations, both animals in group R (H-1, HAC) were slightly retarded in relearning pattern discriminations that the animal in group S (HA) relearned with considerable saving.

Tests. The preceding comparisons between lesion groups and between training groups are based on the data for the three pattern discriminations only. Scores for the red-green[2] and light gray–dark gray discriminations do not differentiate among the groups since all but one operate showed complete retention on both. The occurrence and degree of deficit were thus observed to vary with the particular task employed, irrespective of the effects of operations or training schedules.

If the five discriminations are ranked in terms of the range of trials required by the eight animals to attain criterion on each task preoperatively, the following order is obtained: inverted-erect triangle (160–560), circle-square (50–200), stripes-diamond (0–80), light gray–dark gray (0–30), and red-green (0). Although the reward value of the last four stimulus pairs was reversed for half the animals, the arrangement in terms of preoperative learning rates is the same for all, and is used tentatively to define an order of test difficulty. Postoperatively, this arrangement of the tests is maintained, with the greatest number of failures appearing on the inverted-erect triangle discrimination, numerous instances of less severe deficit on the circle-square and stripes-diamond discriminations, and only a single instance of impairment on light gray–dark gray and on red-green. The observed relationship between deficit and test difficulty is remarkably consistent for all animals, whether trained, postoperatively, from the most through the least difficult tasks (group S) or in the reverse order (group R).

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[2] On the day in which an animal attained criterion on the red-green discrimination, it received two transfer tests presented for ten trials each: (*a*) pale red–bright green and (*b*) bright red–pale green. The four Color-Aid papers used were RT2, GHUE, RHUE, and GT2, respectively. Despite reversals of brightness values, errorless transfer to the previously correct hue was shown by all animals.

DISCUSSION

The severe discrimination impairments observed in the two operates with deep and unintentionally extensive ventral temporal lesions serve to confirm, and extend to other monkeys, results previously reported for baboons. Analysis of the effects of more restricted ablations indicates that damage to ventral cortex alone (three animals) also produced marked deficits on the discriminations. Removal of the hippocampus, on the other hand, either through a minimal incision in the inferior convolution, or through the amygdaloid complex (one animal each), resulted in little or no impairment. Finally, only slight deficit followed combined resection of the polar region and the superior lateral surface (one animal). The results demonstrate that the integrity of the cortex on the ventral surface, as compared with that of other regions in the temporal lobe, is of especial importance for visual discrimination performance.

The degree of impairment produced by the operations varied markedly with the particular task employed. The pattern discrimination that required the longest preoperative learning time yielded the largest number of severe postoperative deficits; the hue discrimination, which required the shortest preoperative learning time, disclosed but a single deficit. These results, obtained with sequence of presentation controlled, confirm the earlier finding of a direct relationship between extent of deficit, as measured in absolute terms, and degree of task difficulty. Order of presentation and test difficulty did interact, however; tasks intermediate in the sequence were relearned more rapidly by animals trained first on the most difficult tasks than by animals trained first on the least difficult tasks.

Deficit on the discriminations was not consistently associated either with retardation in relearning delayed response or with defects in visual fields or acuity. It is further significant that the two operates with amygdala lesions, while relatively unimpaired in their discrimination performance, showed marked changes in their reactions to aversive stimuli. Alterations in avoidance behavior have been observed previously following damage to the amygdala (6, 7); such changes did not appear following lesions restricted to the ventral surface.

It appears from these results that ablation of the ventral cortex of the temporal lobe interferes selectively with performance on visual discriminations, and that damage to this area is primarily responsible for the discrimination impairment shown by animals with temporal lobectomy (1, 4, 5).

SUMMARY

1. Eight macaques were trained preoperatively on a series of visual discriminations of varying difficulty. In addition, they were tested on visual-spatial delayed response and on tasks designed to evaluate extent of visual fields, visual acuity, and reactions to aversive visual stimuli.

2. Following the initial training, ventral temporal cortex was ablated bilaterally in three animals, the hippocampal formation was removed bilaterally in three others, and two animals received operations that served to control for cerebral damage incidental to the hippocampectomy procedures. All animals were then retested on all problems, with the visual discriminations presented in two different sequences.

3. Post-mortem examination of the brains indicated that one hippocampal and one control lesion invaded extensively the area removed in the ventral temporal operates; the six other lesions were accurately placed. Thalamic degeneration findings were con-

sistent with those previously reported for baboons.

4. Ventral temporal resections produced markedly greater impairment on the visual discriminations than did the hippocampal or control operations. The number of postoperative failures and the amount of retardation varied directly with the difficulty of the discriminations, irrespective of the order in which they were presented. Deficit on the visual discriminations was not correlated with impairment on any other task.

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Received July 27, 1953.

EFFECTS OF TEMPORAL NEOCORTICAL ABLATION ON VISUAL DISCRIMINATION LEARNING SETS IN MONKEYS

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It has been repeatedly demonstrated that bilateral extirpation of the temporal neocortex affects the retention of visual discrimination in monkeys (1, 4, 5, 6, 12, 13). The nature of the visual disturbances and its underlying neural mechanisms are yet to be elucidated. Recent experimental results suggest that monkeys with temporal lobe removals may have normal color, brightness, and pattern vision per se, and that only the learned habits of differential reactions to colors, brightnesses, and patterns are lost (4, 6). Even in these cases, specific habits may not be entirely abolished after the surgery. They are only temporarily suppressed and may be restored without any specific retraining by allowing the monkey to learn other, new visual discriminations (5). Thus, it appears that the detrimental effect of temporal lesions is neither a disruption of the visual capacities nor a demolition of the memory traces of visual habits. The loss of the learned response without either sensory defect or memory impairment is a mysterious paradox. One possible explanation is that what has been disturbed may be the animal's general set in the formal training situation; the *S* may lose its ability to comprehend the essentials inherent in a discrimination problem.

The present study is a further attempt to analyze, with regard to this hypothesis, the visual symptoms resulting from temporal lobe lesions. The possibility that the cortical injury affects only the monkey's general set for visual discrimination learning is investigated. The apparent loss of individual habits may be secondary to the animal's failure to maintain a proper set. The ability to establish what Harlow (8) has defined as discrimination learning sets is used as a behavioral index of the animal's general set. The success in this problem requires not the remembering of specific discrimination habits, but the realization of a general principle. The animals learn to use the first trial to gain information (to react to the visual aspect of the discriminanda and to discover which one of the two signifies reward), and they respond accordingly on the second trial of each new problem. The effects of temporal neocortex removal on the retention of discrimination learning sets are reported here.

METHOD

Three immature monkeys (*Macaca mulatta*) were used. They were trained preoperatively to acquire a visual discrimination learning set for objects and another learning set for patterns. The objects differ from each other in color, shape, and size. The patterns are India ink drawings on 3-in. by 5-in. white cards; they differ only in what is painted on the card, ranging from simple geometric figures to complex nonsense line drawings. Two monkeys (no. 1 and 2) were trained on the pattern discriminations first, and on the object discriminations second. The third animal (no. 3) was given the object problems first, followed by the pattern problems. The procedure used to establish the learning sets was that described by Braun *et al.* (2). The preliminary training consisted of 67 discriminations: 50 trials for each of the first 8 problems, 10 trials for the next 24 problems, and 6 trials for the last 35 problems. The main part of training consisted of either 100 or 450 discriminations, each presented for 3 trials.

All three animals were trained on a third problem, a trial-unique, nonspatial, delayed response. The animals were required to choose that one of two objects under which a piece of food was previously shown. A new pair of three-dimensional objects was used for each trial. During the delay interval, the two objects may remain in the same position or be exchanged with each other. The food reward was shifted or not accordingly, always being under the object that had been baited. After preliminary adaptation to the experimental situation and training without a screen during the delay interval, all animals were given 50 trials with each of the two conditions: 5-sec. and 10-sec. delay, with an opaque screen concealing the stimulus objects during the delay interval. This problem was included to test whether the effect of temporal lesions is specific to performance in visual discriminations alone, or whether it may also involve the ability to perform delayed response, which is consistently impaired after prefrontal removals.

Two months after completion of the original training, the monkeys were tested for preoperative retention of object- and pattern-learning sets. Thirty new object discriminations and 30 new pattern discriminations, three trials for each problem, were given. The animals were then subjected to bilateral temporal neocortical extirpation in one stage. All operations were performed under Nembutal anesthesia with aseptic technique. The cortex was removed by aspiration. The animals recovered uneventfully.

Fourteen days after surgery, postoperative retention tests on object- and pattern-learning sets were given (30 pairs of objects and 30 pairs of patterns, three trials for each discrimination). Since all *S*s failed in the retention tests, they were given retraining on learning set for patterns by the same preoperative procedure. They were tested on the nonspatial delayed response as the last problem.

After the completion of the experiment, monkeys no. 1 and 2 were used in another study. Their prefrontal areas were ablated in this terminal experiment, which will be reported elsewhere. Their body weights at the time of sacrifice were: no. 1 (female), 3.6 kg.; no. 2 (female), 4.3 kg.; no. 3 (male), 3.3 kg. The brains were fixed and sectioned coronally in 50-μ thickness. Every tenth section was saved and stained with thionin. The extent and location of the cortical lesions were reconstructed and the retrograde degeneration in the thalamus determined. The histological procedure, method of reconstruction, and the criterion of retrograde degeneration have been described in a previous report (1).

RESULTS

Anatomical Data

Figure 1 gives the reconstructions of cortical lesions of the three animals as viewed from the lateral side of the hemispheres, and shows the cross sections through the lesions and the degenerated thalamic pictures. All the temporal lesions are confined to the cortex, with only slight damage to the underlying white matter. The medial structures of the temporal lobe are intact. Retrograde degeneration appears in the posterior part of *n. pulvinaris medialis* of all animals. In addition, there are small degenerated zones in the medial geniculate of monkey no. 3, and in the *n. ventralis posteromedialis* of monkey no. 1. These anatomical findings are no different from previously reported cases (3). The lesions in the prefrontal regions of monkeys no. 1 and 2 were made in connection with another experiment after the completion of the present study. It should be noted that because of the short postoperative survival period, no degeneration is apparent in the *n. medialis dorsalis* of monkey no. 1, and only a small atrophied area in the left *n. medialis dorsalis* of monkey no. 2.

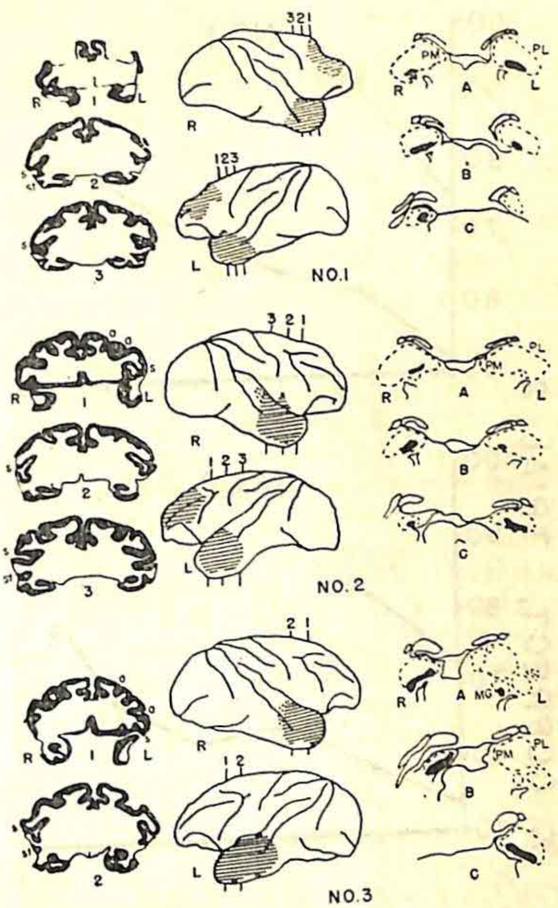

FIG. 1. Records of lesions in *S*s no. 1, 2, and 3. Reconstructions of the location and extent of cortical lesions are shown on the lateral surface of the hemispheres. Complete destruction is indicated by hatching; partial destruction, by stippling. The positions of the cross sections (1, 2, 3) through the lesion are shown by the numbered lines on the surface drawings. The lesions in the prefrontal region of *S*s no. 1 and 2 are made after the completion of the present study, which will be reported elsewhere. Sections through the posterior thalamus (*A*, *B*, *C*) are also presented; its degenerated zones are indicated by solid black. *R*, right; *L*, left; *a*, arcuate sulcus; *st*, superior temporal sulcus; *s*, Sylvian fissure; *MG*, medial geniculate; *PL*, *n. pulvinaris lateralis*; *PM*, *n. pulvinaris medialis*.

The Formation and Transfer of Discrimination Learning Sets

The course of developing the learning sets of the three *S*s resembles that described by Harlow (8) and Braun *et al.* (2) for monkeys, and that of Hayes *et al.* (11) for chimpanzees. There is an orderly improvement in the acquisition of the successive discriminations, until the second trial correct reaches 80 or 90 per cent in the last hundred problems. The pattern discrimination appears to be more difficult than the object discrimination. This is indicated by the slower rate of improvement and the lower level of efficiency finally achieved in pattern problems. Both these

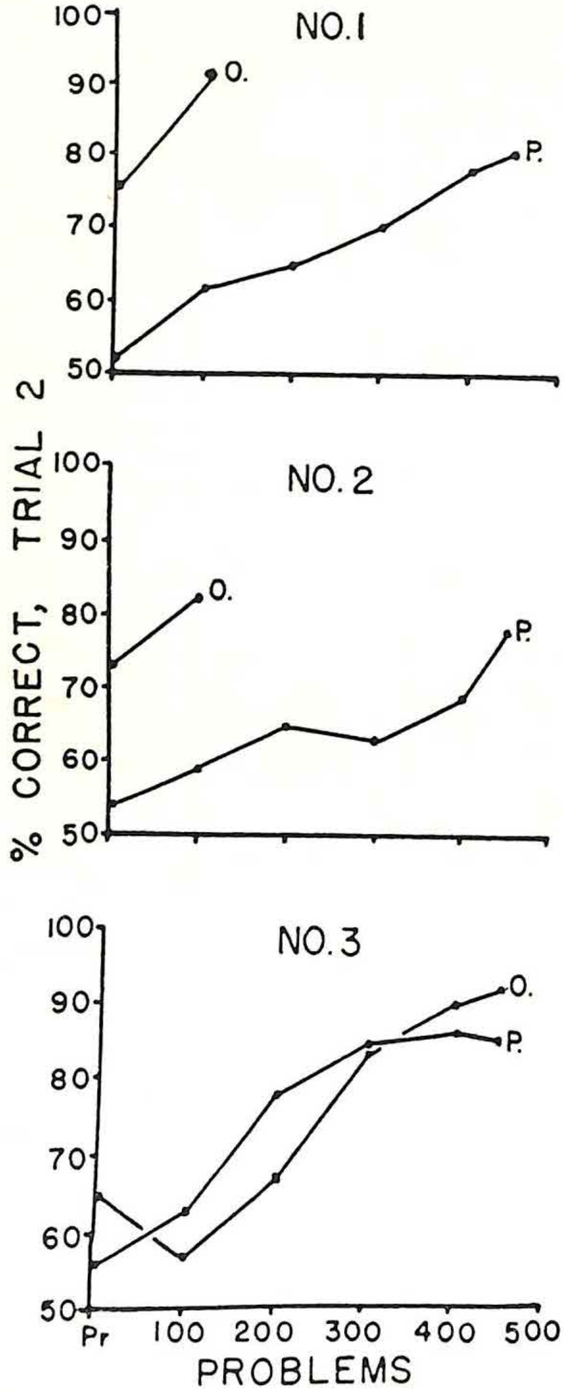

FIG. 2. Formation and transfer of learning sets. Percentages correct on the second trials are plotted as a function of successive problem blocks. Subjects no. 1 and 2 learned the pattern discriminations before the object discriminations. Subject no. 3 learned the object problems first. *O*, object discriminations; *P*, pattern discriminations; *Pr*, 67 problems in the preliminary training.

points are shown in Figure 2, where the development of learning sets is plotted as a function of problems, i.e., the percentage correct on the second trial in successive blocks of problems. The curves for pattern discriminations of all three monkeys are below those for object discriminations of Harlow's and Braun's monkeys, and of Hayes's chimpanzee (compare Fig. 3*A* in 11).

Figure 2 also shows the different degrees of transfer between learning sets for different types of visual discriminations. There is a high degree of positive transfer from pattern discriminations to object discriminations (monkeys no. 1 and 2), but much less transfer from the object to pattern problems (monkey no. 3). In fact, after the animals have had a learning set for pattern discriminations, they can acquire a learning set for objects within about one hundred problems. These results are in agreement with those of Harlow and Warren (10). Their monkeys also showed a large positive transfer effect from learning sets of planometric patterns to stereometric objects. The relatively less transfer from object to pattern discriminations of monkey no. 3 is confirmed by the unpublished data on another monkey.

Retention and Reacquisition of Learning Sets

Figure 3 gives the data on pre- and postoperative retention of learning sets. All animals showed perfect retention of learning sets after a period of two months, before the operation. After bilateral temporal neocortical ablation, the animals lost the learning set for pattern discriminations. Moreover, they were not able to regain the set even after retraining on more than five hundred problems presented by the same procedure used preoperatively. These animals, at the same time, still had the ability to learn individual pattern discriminations. They learned to discriminate a black diamond (positive) vs. black and white horizontal striations within the normal time (around 200 trials) after they had failed to re-establish the learning set.

Monkey no. 1 did not lose the learning set for object problems after the surgery. The other two animals lost the set postoperatively, but regained it with very little retraining. Monkey no. 2 re-established the set after 32 object discriminations (50 trials per problem for the first 8 problems, and 10 trials each for the other 24 problems), and monkey no. 3, after only 8 problems (50 trials each).

Nonspatial Delayed Response

Two monkeys retained the ability to perform nonspatial delayed response after temporal neocortical ablations; the third *S* lost the ability and did not regain it within the limits of training. Preoperatively, monkey no. 1 performed 84 per cent and 86 per cent correct for the 5-sec. and 10-sec. delay (50 trials each). After the operation, the scores were 86 per cent and 78 per cent. The percentages correct for the 5-sec. and 10-sec. delay of monkey no. 3 were 90 and 88 preoperatively, 80 and 72 postoperatively. Monkey no. 2 performed 80 per cent correct (5 sec.) and 84 per cent correct (10 sec.) before the surgery, but postoperatively performed at a chance level at the end of 500 trials with 5-sec. delay *without* the opaque screen, and at the end of an additional 200 trials for 5-sec. delay *with* the screen.

DISCUSSION

The present results demonstrate that temporal lobe lesions affect selectively the retention of learning sets for different types of visual discriminations. All operated animals showed good retention of a learning set for object discriminations, but they failed to reacquire a set for pattern problems. If the formation of learning sets is indicative of the monkey's general set to learn visual tests, then these results rule out the hypothesis advanced earlier that the loss of a general set is primarily responsible for the visual symptoms produced by temporal removals. Two possible explanations of this differential effect on object and pattern learning sets may be suggested: (*a*) There are separate learning sets for different visual problems. The monkeys are required not only to have a general set, but also to react to the relevant cues specific to a class of stimuli. The operation perhaps destroys one and not the other of these two sets. (*b*) The pattern discriminations are more difficult tests than object problems, and temporal lobe injury will disturb performance on difficult tasks more than on easier ones. This latter interpretation is in agreement with the findings that large posterior lesions in the monkey's association cortex affect pattern more than object discriminations (9, 14). However, the mechanism involved in the temporal damage which disturbs the ability to

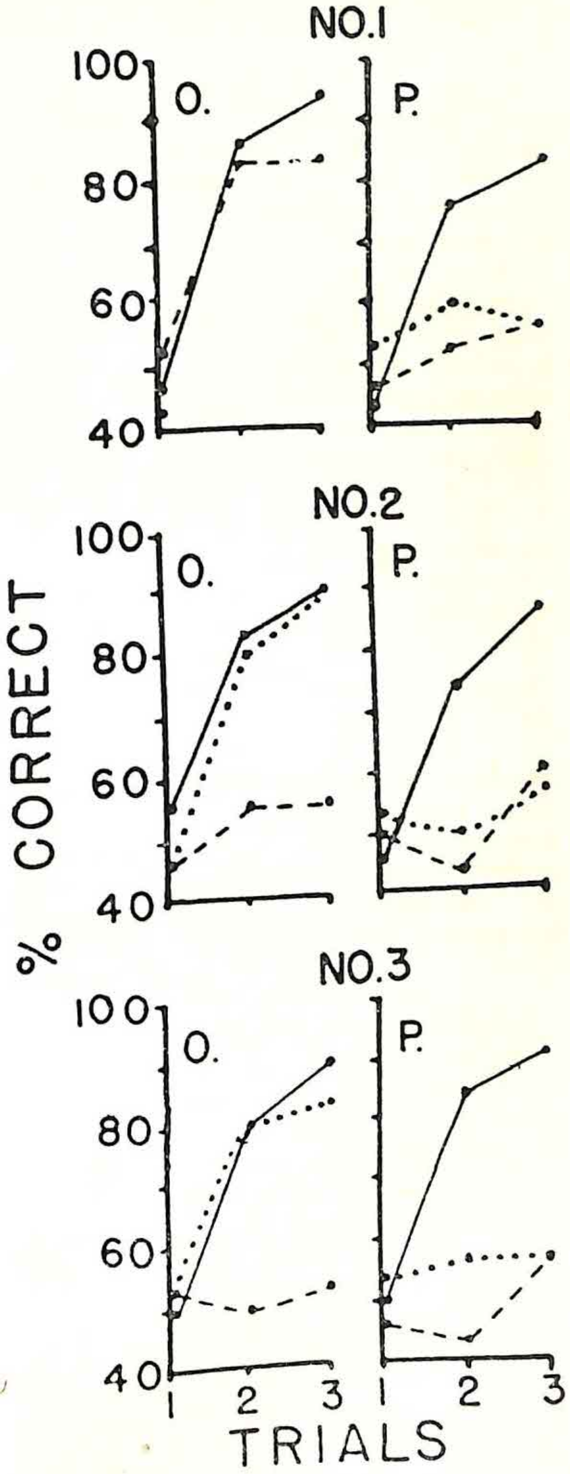

FIG. 3. Pre- and postoperative retention and the postoperative relearning of learning sets. Straight lines, preoperative retention; dashed lines, postoperative retention; dotted lines, the last 30 problems in retraining; *O*, object discriminations; *P*, pattern discriminations.

perform more difficult discriminations is not known. It may be that there are some interferences of the animal's visual attentiveness after the surgery.

The good retention of the learning set for object discriminations by these monkeys is unexpected in view of the results reported by Riopelle *et al.* (13). They found that temporal lobectomized monkeys could not be trained to form learning sets for object problems. Also, monkeys did not retain the previously established set for objects after such a lesion.[1] This discrepancy may be due to the differences in the brain injuries. The lesions in the present series of monkeys were confined to the neocortex. Riopelle *et al.*, without anatomical verification, reported damage to both the neocortex and the deep temporal structures in their monkeys. Further researches are needed to clarify this point.

The failure of monkey no. 2 to perform nonspatial delayed response postoperatively indicates that, in some monkeys, the effects of temporal lobe extirpations are not restricted to visual problems alone. This case, together with those reported in earlier studies, suggests again that functional representation within the association cortex may not be strictly localized. Although the ability to perform the delayed response problem is focally dependent on the prefrontal region, it may involve other cortical areas as well (7).

SUMMARY

Three immature monkeys (*Macaca mulatta*) were trained preoperatively to form learning sets for visual object discriminations and for pattern discriminations. They were also given a nonspatial delayed response problem.

After bilateral temporal neocortical ablations, all animals lost the learning set for pattern discriminations, and were not able to regain it even after prolonged retraining. Two monkeys (no. 2 and 3) also lost the learning set for object problems, but reacquired this with a large amount of saving. The third animal (no. 1) did not lose the learning set for object discriminations after the operation.

Postoperatively, one monkey (no. 2) lost the ability to perform the nonspatial delayed response, whereas the other two (no. 1 and no. 3) showed good retention on this problem. These results are briefly considered in relation to the nature of the visual defects following temporal lobe lesions.

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Received September 9, 1953.

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ROLE OF THE CEREBRAL CORTEX IN TEMPERATURE DISCRIMINATION IN THE RAT[1]

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In recent years, considerable interest has been shown in the role of the cerebral cortex in various aspects of cutaneous sensitivity in such animals as the rat (8, 10, 11), cat (9), dog (2, 3), and monkey (4, 5). One aspect that has been largely overlooked, however, is temperature sensitivity. For many years we have known that the hypothalamus is an important regulation center for temperature, but we know relatively little about the role of higher neural centers, such as the cerebral cortex, in temperature discrimination. It was the purpose of this study to determine what role, if any, is played by the cerebral cortex of rats in the discrimination of temperature.

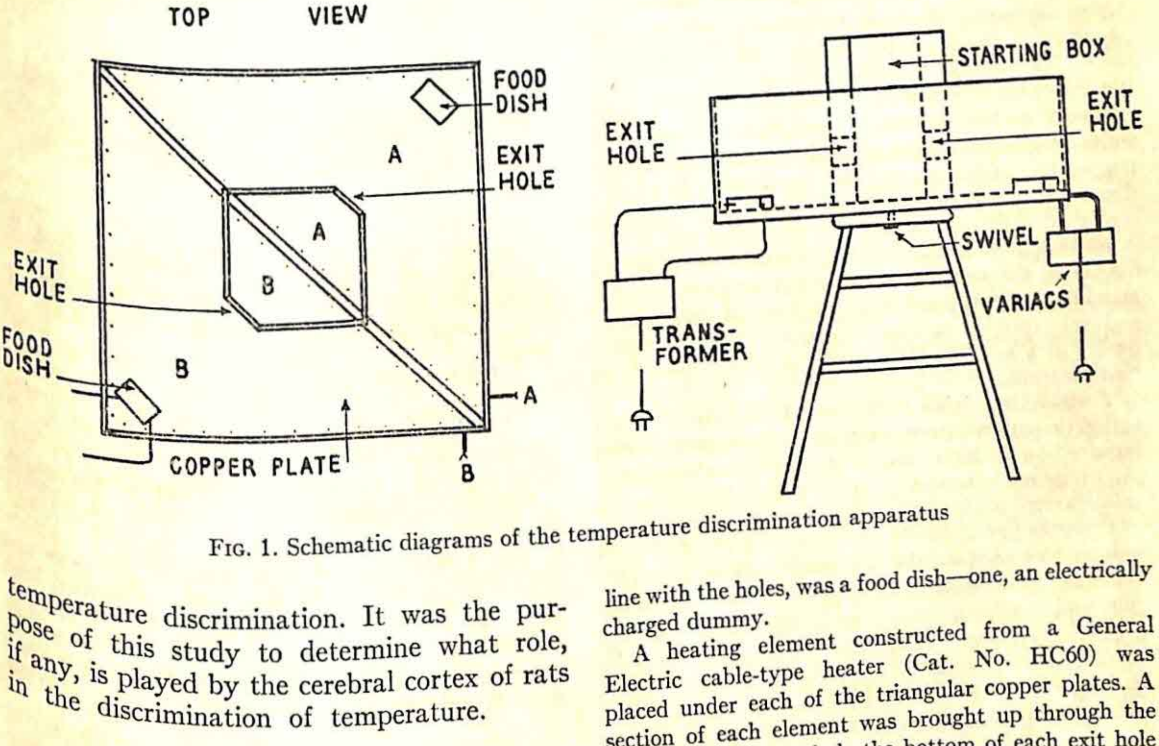

FIG. 1. Schematic diagrams of the temperature discrimination apparatus

METHOD

Subjects

Twenty naive male rats, all descendants of the Lashley strain, were used as *S*s. When the study began, they were three months old and averaged 205 gm. in weight.

Apparatus

The apparatus consisted of an open wooden box, 3 ft. square and 1 ft. high (see Fig. 1). The bottom of this box was covered by a copper plate, cut diagonally and separated by a ½-in.-wide wooden runner that served as an insulator between the two triangular halves (Plates *A* and *B* in Fig. 1). Centered in the large box was a smaller box, 1 ft. square and 1½ ft. high. In the corners of the smaller box that were not cut by the wooden insulator, and 4 in. above floor level, were two holes just large enough for a rat to climb through. In each corner of the larger box, directly in line with the holes, was a food dish—one, an electrically charged dummy.

A heating element constructed from a General Electric cable-type heater (Cat. No. HC60) was placed under each of the triangular copper plates. A section of each element was brought up through the copper plates to encircle the bottom of each exit hole in such a way that a rat climbing through the hole would come into contact with the element. Each element in turn was connected to a Variac. This Variac provided an effective means for controlling the temperature of each element independently. Each plate was provided with a thermometer. The whole apparatus rested on a laboratory stool and could be rotated through 360° by means of a swivel pin transfixed through the stool and the base of the box.

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[1] This study, supported by a grant from the National Research Council, Canada, was carried out in the Department of Psychology, McGill University.

Procedure

Preliminary training. Ten days prior to training, the rats were blinded by enucleation and were put on a 24-hr. feeding schedule. Then they were placed in the apparatus for 1 hr. per day for a week and allowed to become familiar with it. After this period of habituation, the training sequence began.

One of the copper plates was heated to 55° C.; the other was kept at 25° C. (approximate room temperature), thus forming a temperature difference of 30° C. between the two sides. Food was placed in both dishes. Since the object of training was to teach the animals always to avoid the warmer plate, the food dish on the warmer side of the box was covered with wire mesh and electrically charged. Each rat, in turn, was placed in the small, inner starting box, where the same temperature differences prevailed as in the larger outside box. To obtain food it was necessary for the rat to climb through one of the two holes and to run over to the dish on the cooler side (positive stimulus). An error was scored if the rat went to the food dish on the warmer side, regardless of what hole it had climbed through. After each trial the animal was removed and the apparatus was rotated through 180°. The temperatures of the two copper plates were varied from day to day according to the Gellermann sequence: one day Plate *A* would be the warmer; another day, the cooler. Each animal was given ten trials per day until it reached the criterion of at least 80 per cent correct responses on two successive days. After the rats had learned the relatively crude discrimination (30° C.), the temperature of the warmer side was reduced to 45° C., thus forming a difference of 20° C.; training was then continued until the criterion was again reached.

Sham operation. After reaching criterion on the 20° C. difference, the animals were divided into two groups, matched as far as possible on the basis of their scores, and subjected to a sham operation. This consisted merely of a mid-line incision of the scalp with subsequent suturing.

Postsham retraining. Following a 14-day recuperation period the animals were put back in the apparatus and retrained on the 30° C. and 20° C. discriminations to the same criterion as before. After completing retraining, all animals were subjected to cortical operations.

Operative procedure. In all operations Pentobarbital sodium was used as the anesthetic. When necessary this was supplemented with ether. After incision of the skin and overlying fascia, the bone over the desired area was removed and the cortical tissue removed by suction with a small glass pipette attached to an aspirator. One group of animals was subjected to removal of somatic areas I and II, and the other group, to removal of cortical tissue both anterior and posterior to the somatic areas (the frontal-occipital group). All operations were bilateral. Six rats were lost during the course of the study, leaving a total of 14 animals with completed records.

Postoperative testing. After the operation, a period of 14 days was allowed for recovery. The animals were then reintroduced to the apparatus and tested on the 30° C. and 20° C. temperature differences. They were also tested on a 10° C. discrimination, which had not been done previously with these animals. In a preliminary survey it had been established that the finest temperature difference that could be discriminated was 10° C.

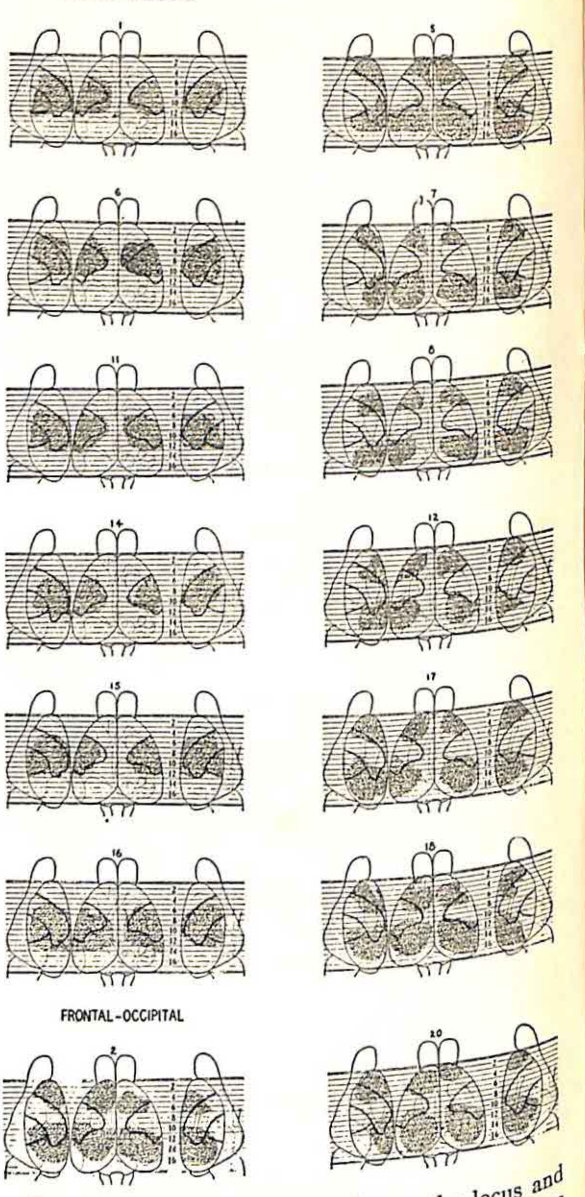

FIG. 2. The stippled area indicates the locus and extent of cortical destruction, and the heavy lines show the location of somatic areas I and II. The differential experimental groups are designated by appropriate headings. The animal's experimental number is shown above each diagram.

Post-mortem procedure. On completion of the postoperative testing the animals were killed by injection of a formalin perfusion fluid into the left ventricle of the heart. The brains were then removed, fixed in celloidin, sectioned at 45 mμ, stained, mounted on slides, and the lesions plotted on the standard Lashley diagrams.

RESULTS

The anatomical reconstructions of the brains are shown in Figure 2; behavioral results, in terms of errors to reach criterion, are summarized in Tables 1 and 2. All scores shown in the tables include the criterial trials.

Preliminary (Control) Data

Before the start of the present experiment a preliminary study had been conducted with 12 rats to determine the finest temperature difference that they were capable of discriminating. This was found to be 10° C. for the apparatus used. The results for the individual animals are shown in Table 1. It can be seen that the animals made an average of 5.5 errors before they learned to discriminate a difference of 10° C. (35° C.–25° C.). With differences finer than this, the scores became a matter of chance. These preliminary data are presented in some detail because of their importance in interpreting the results of the present experiment.

TABLE 1

Number of Errors Made by Animals of Preliminary Study before Meeting Learning Criterion on Temperature Discrimination of 10° C. (35° C. – 25° C.)

RAT NO.	ERRORS
1	3
2	4
3	3
4	4
5	9
7	1
8	10
9	3
11	8
12	20
13	1
14	0
Mean	5.5
SD	5.4

Operative Data

Table 2 shows the preoperative and postoperative performance of animals subjected to removal of various parts of the cerebral cortex. It can be seen that animals with ablations of the frontal and occipital areas of the cortex show a considerable postoperative saving in error scores as compared with their preoperative scores in learning the 30° C. and 20° C. discriminations. Postsham and postoperative scores for these two temperatures are about the same. We also note that this operated group of animals learned to discriminate the 10° C. difference as quickly as did the normal group of 12 animals in the preliminary study (5.7 errors versus 5.5 errors; $p > .90$). We may therefore conclude that removal of cortical tissue anterior and posterior to the somatic-sensory areas does not cause a loss in the ability to discriminate temperature differences at or above 10° C.

Animals with lesions of somatic areas I and II, like those with frontal-occipital lesions, show a considerable postoperative saving in errors in relearning the 30° C. and 20° C. discriminations as compared with initial

TABLE 2

Number of Errors Made before Meeting Learning Criterion on Temperature Discriminations of 30° C., 20° C., and 10° C. before and after Ablation of Specified Cortical Areas

FRONTAL-OCCIPITAL AREAS								SOMATIC AREAS I AND II							
Rat No.	Initial		Postsham		Postoperative			Rat No.	Initial		Postsham		Postoperative		
	30° C.	20° C.	30° C.	20° C.	30° C.	20° C.	10° C.		30° C.	20° C.	30° C.	20° C.	30° C.	20° C.	10° C.
2	1	3	0	4	1	0	4	1	3	26	1	2	6	3	3
5	3	0	1	0	3	2	19	6	3	24	0	16	0	2	3
7	3	0	0	0	0	0	4	14	0	0	0	0	0	0	1
8	23	2	0	0	0	0	8	15	2	4	0	0	0	0	0
12	22	20	0	19	4	1	1	11	24	23	1	17	2	34	28
17	1	3	0	4	0	1	3	16	15	12	1	2	3	2	6
18	0	0	0	1	0	1	3								
20	4	12	0	2	6	3	4								
Mean	7.1	5.0	0.1	3.7	1.7	1.0	5.7		7.8	14.8	0.5	6.2	1.8	6.8	6.8
SD	8.9	6.8	0.3	5.9	2.1	1.0	5.2		5.6	10.1	0.3	5.1	2.2	13.2	9.6

learning; the amount of saving is of approximately the same magnitude for both groups. Again, the postsham and postoperative scores for the two temperatures are about the same. From Table 2 we see that these animals made an average of 6.8 errors in learning to discriminate the 10° C. difference. Although this error score is somewhat higher than that made by the normal group of 12 animals (5.5 errors) for the same temperature discrimination, the difference is not statistically significant ($p > .70$). As with the previous group, it becomes apparent that removal of somatic areas I and II produces no loss in ability to discriminate temperature differences at or above 10° C.

DISCUSSION

Since information on the role of the cerebral cortex in the discrimination of differences in temperature is almost totally lacking, this study attempts to explore the problem.

The foregoing results clearly indicate that removal of somatic areas I and II has no deleterious effect on the retention or relearning of temperature discriminations at or over 10° C; furthermore, ablation of cortical tissue both anterior and posterior to the somesthetic cortex has no adverse effect on such discriminations. This lack of impairment is evidenced by the absence of amnesia and by the considerable postoperative saving in error scores by both groups of animals. Apparently, then, no part of the cerebral cortex of the rat is essential for discriminating temperature differences.

The results obtained in this investigation are supported by two lines of evidence: First, Adrian (1), using the evoked-potential technique, which has proved very fruitful in mapping other sensory projection areas, was unable to record any cortical potentials after thermally stimulating various parts of the body surface of cats; secondly, neuroanatomists, using cytoarchitectonic and retrograde degeneration methods, have repeatedly failed to localize the cortical end station at which temperature sensation fibers are thought to terminate. It has been known for some time that the second-order neurons of the lateral spinothalamic tract reach the level of the thalamus and that most of these fibers terminate in the posteroventral nucleus. Although it has been assumed that the third-order neurons arising from this nucleus convey temperature impulses to the somesthetic cortex, there is no direct evidence to show that this is the case (see Ranson and Clark, 6). Walshe (7) goes so far as to state that the lateral spinothalamic tract does not continue on to the cerebral cortex and that impulses carried by this tract reach "consciousness" in the thalamus.

In conclusion, the present investigation has demonstrated that in rats the cerebral cortex is not necessary for the discrimination of temperature differences either at or above 10° C.

SUMMARY

An apparatus was constructed in which rats could be trained to discriminate temperature differences of 30° C., 20° C., and 10° C.

The experiment began with 20 rats. After blinding, the animals were trained to discriminate temperature differences of 30° C. and 20° C. On the basis of these initial scores they were divided into two groups, both of which were then subjected to a sham operation and allowed a 14-day recuperation period. Following this they were retrained on the same temperature differences to criterion, as before. One group was then subjected to ablation of the frontal-occipital areas of the cerebral cortex, while the other group was subjected to ablation of somatic areas I and II. After a 14-day recovery period both groups were tested on temperature discriminations of 30° C., 20° C., and 10° C. Fourteen rats survived the experiment.

No impairment of temperature discrimination occurred following the bilateral removal of either the frontal-occipital cortex or somatic areas I and II.

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Received September 23, 1953.

STUDIES IN THE NEUROPHYSIOLOGY OF LEARNING: I. EFFECT OF BRAIN STIMULATION RATE DURING RUNS ON MAZE PERFORMANCE IN THE WHITE RAT

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Twenty years ago the senior author published a monograph setting forth a neurophysiological theory of the learning process (2). This theory was based primarily on two neurophysiological parameters, viz., frequency of nerve impulse volleys and their duration. Since that time, the importance of stimulation rate on nerve function has been amply demonstrated (6, 8). Furthermore, electronic developments in the last decade have made it possible to design and construct equipment that permits at least an approximate experimental test of the theory. This is the first of a series of experiments directed to an investigation of the influence of stimulation rate, duration, and locus of cerebral excitation on the learning processes in some mammals.

The present report is concerned with a study of the differential effect of two rates of brain stimulation (75/sec. and 300/sec.) on maze learning in the white rat. Strength of stimulus was the same for the two frequencies, and the duration of each pulse was approximately the same.

METHOD

Apparatus

Electronic. The transmitter system used is of the pulse-modulated radar type and has been described elsewhere (4). Since the original publication (4), the pulsing characteristics of the equipment have been altered. It is now capable of repetition rates between 20/sec. and 2400/sec. The pulse duration is variable between 3.00 msec. and .1 msec., but pulse duration is not completely independent of pulse repetition rate. The carrier frequency is 221 m.c. The miniature receiver borne by the animal is essentially a crystal set and has also been described (3). In the present experiment, however, a 1N23-B crystal has been substituted for the 400-A crystal previously employed. The crystal serves to rectify the bursts of high frequency waves into direct current pulses of rectangular shape.

Surgical. The general surgical procedure has been described (3). The electrodes were fashioned from stainless steel wire .031 in. in diameter, and were ground down to a conical shape that ended in a fairly fine point. Each electrode was 5 mm. long and insulated except at the point, which was bared for a distance of 1 mm. No attempt was made at precise placement of the electrodes in the present experiment; attempts at critical placement will be made in later investigations when and if this is necessitated by experimental requirements. The two electrodes were inserted through two holes in

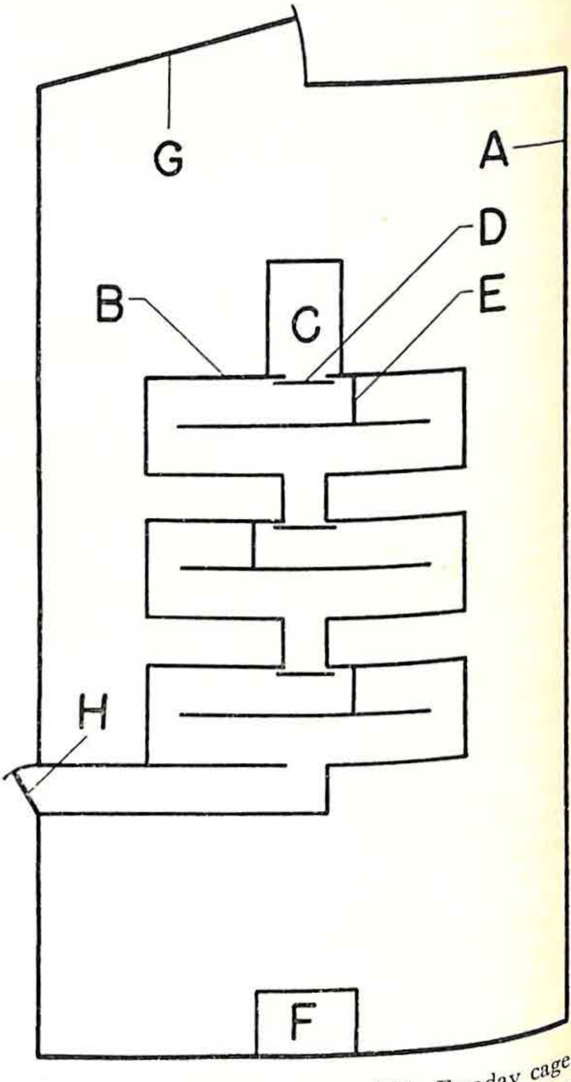

FIG. 1. Ground plan of maze within Faraday cage. (*A*—Faraday cage [123 in. by 64 in. by 60 in.]; *B*—maze unit [12 in. by 38 in. by 8 in.]; *C*—food box; *D*—sliding door; *E*—portable barrier; *F*—oscillator; *G*—cage access door; *H*—maze entrance door.)

the skull, .029 in. in diameter, drilled symmetrically on either side of the mid-line and about 1 mm. ahead of the forward edges of the ears (9, p. 330). The holes were roughly 5 mm. apart, and the conical shaped electrodes were forced through them. This provided a satisfactory "press fit," which kept the electrodes firmly in place. In those specimens examined, the electrode tip had penetrated slightly more than 1 mm. below the surface of the cerebral mass.

Maze. The ground plan of the maze is shown in Figure 1. The alleys were 8 in. deep, and the whole structure was covered by a leucite sheet, which yielded, simultaneously, good visibility and freedom from electromagnetic shielding. The depth of the alleys prevented any impact between the antenna on the rat's back and the covering over the maze. Doors were placed between maze units to prevent retracing. These doors, together with the blocks used in the cul-de-sacs, were of leucite and quite transparent. Since the maze was placed inside a double-shielded cage, the animals were introduced into the maze through a small slit door, which was then immediately closed. Once the rat had arrived at the food box and eaten for the allotted period of time, *E* entered the cage through the large door and removed *S* for the next run.

Procedure

In preliminary experiments it was found that animals showed tremendous individual differences in their preferences for certain turns in the maze. Since the maze distances were relatively small (because of the size of the cage), some animals would enter a cul many times before abandoning it. It was therefore decided to institute a period of preoperational training sufficient to guarantee that all animals had "learned" the maze pattern L-R-R. After the period of maze adaptation (seven days), the animals were given 60 runs in the maze with this pattern at the rate of five runs per day. At the end of this time, all the animals were found to have "learned" the pattern, as judged by a not too rigid criterion. The purpose of the preoperational procedure was to give all animals a fairly homogeneous background of maze training and alley dispositions. While the success of this maneuver cannot be considered complete, in the sense that all the animals possessed the same degree of fixation for any specified turn, it is felt that it did bring the rats closer to a common point of origin for the experiment proper.

The day after completion of the preliminary training, the rats were operated and the receiving equipment was installed. Twenty-four hours later the animals were placed in the maze and permitted to run, in the absence, however, of any power in the field. The animals were given three runs.

On the second day after the operation, the animals were divided into three groups: (*a*) Low Frequency (LF) (75 pulses/sec.; pulse width, .975 msec.); (*b*) High Frequency (HF) (300 pulses/sec.; pulse width, .5 msec.);[1] and (*c*) Operated Control (OC) (receiver installed but no power present in the field). There was a fourth group, which is called the Normal Control (NC). This group was in every respect treated as the other three, except no surgery was performed. All the animals were now given five massed runs daily on the maze pattern R-L-L, i.e., the mirror image of the preoperational pattern. This was continued for five days.

The mechanics of the experiment were such as to preclude the possibility of performing it at the same time on all the animals to be used. The surgery on each animal required an average of 40 min. If we wished to use a total *N* of about 30 for the three operated groups, it would be necessary to stagger the procedure. It was decided that the interest of experimental design would be best served by a process of replication. Each experiment comprised 8 animals—2 in each of the four groups—and was replicated once every three or four weeks until a satisfactory total *N* had been accumulated. Some of the animals from the operated groups were lost because of equipment failure; also, if a sufficient number of animals was not available for a given experiment, we stinted on the NC group rather than the others. This resulted in an unequal *N* for the four groups of animals used. All the animals were males and between 90 and 120 days old.

On the first of each day's runs, the operated animal's receiver was tested for electrical continuity by measuring the resistance between the electrodes. A special device was constructed and utilized to measure the resistance between the cerebral electrodes. By screwing this little unit on the "smoke stack" (cf. 3, p. 536), it was possible to obtain a resistance reading with no difficulty. Whenever this value strayed markedly from the range 5,000 to 10,000 ohms, the animal was discarded, since this constituted prima-facie evidence that some defect had developed in the receiver unit. If the continuity tests were satisfactory, the animal was entered into the maze through the slit door in the cage. As soon as the door was closed behind the rat, the power was turned on at the predetermined frequency and left on until *S* had entered the food box. It was permitted to eat for 20 sec., and then returned for the next run.

The power level to be used in the experiment had been the object of separate preliminary investigation. To use too little power might result in failure to stimulate the brain; to use so much as to result in motor response (3) would be equally undesirable in a learning experiment. Preliminary explorations had established the mean threshold for motor responses when electrodes were placed in the brain area in question. The power level employed was kept well below this threshold. In a few instances, however, a rat showed motor response to the cerebral stimulation; in these cases, the power level was lowered still further for the particular animal.

RESULTS

The results to be reported here are primarily in terms of errors. An error was scored whenever the rat's head and shoulders penetrated a cul. Successive entries into the blind alley of a given unit were quite common and were, of

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[1] The design of the equipment was such that it was impossible to obtain equal durations for these two frequencies (cf. 4, p. 264).

TABLE 1

Average Number of Errors Made by Each Rat per Day (Five Runs) and Group Means for All Five Days

GROUP	N	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	GROUP MEAN (for 5 days)
Normals	9	11.9	4.0	3.3	1.8	2.9	23.9
Operated controls	11	12.8	7.6	4.3	2.1	2.1	28.9
High frequency	12	13.7	5.6	4.0	3.4	2.1	28.8
Low frequency	14	14.0	6.8	5.4	4.7	3.8	34.7

course, summed to constitute the animal's error score for the run.

Daily average errors are given in Table 1. A simple analysis of variance based on the total errors for the five days (25 runs) yielded an F of 2.92, which for 3 df is significant at the 5 per cent level. The t test was applied to the various comparisons among the four groups; the comparisons are in terms of the total number of errors made on the five days (25 runs). Of these six comparisons, only one is significant when a two-tailed test is used, namely, that between the NC and the LF groups ($t = 2.95$); this, however, is significant at the 1 per cent level.

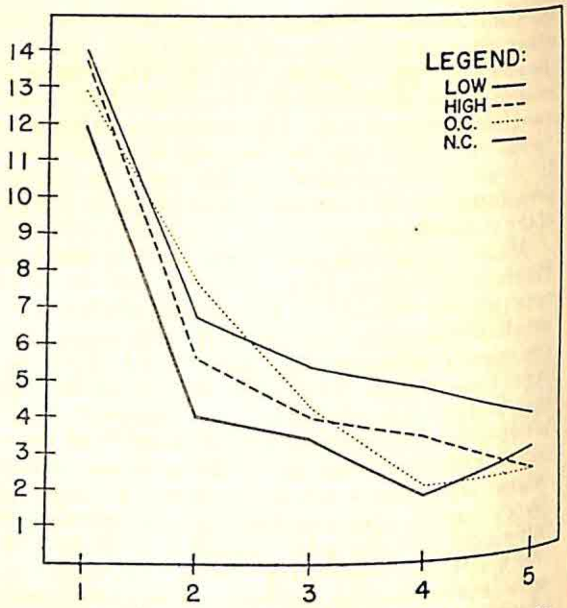

FIG. 2. Mean number of errors made per day by the four groups

A graphical representation in terms of the mean number of errors per day (five runs) made by the various groups of animals is shown in Figure 2. Inspection of these graphs raises two questions: (*a*) Are the mathematical functions describing the four curves identical except for constant terms? (*b*) If any pair of curves has the same function, is the difference between successive pairs of means significantly greater than zero?

These problems may be treated by Lindquist's method of trend analysis (7). Our prime interest here is to compare the three operated groups, since we are concerned only incidentally with the effects of the operation as such. To insure homogeneity of variance, it was found necessary to submit the scores to a square-root transformation. The results of these comparisons are summarized in Table 2. It will be noted that the mathematical function for the HF group is identical to that for the LF group, but that the difference between the successive pairs of means is significantly greater than zero at the 5 per cent level. This comparison did not yield significant differences when the total errors for the five days were used. All other comparisons yielded insignificant differences except that between the OC and LF groups. The difference here reached the 7 per cent level of significance.

While the Lindquist method is a most useful device for dealing with the comparisons of empirical curves, the present investigation could profit by a procedure that answers the question: Is learning *rate* affected by cerebral stimulation rate? The rate of learning should be freed from the absolute level of the learning curve itself. This would make it theoretically possible, for example, for a "duller" group of animals to show a faster rate of improvement than a "brighter" group, even though its performance at a given time remained inferior to that of the latter group. The procedure, furthermore, should yield a simple index number that may be easily compared under various experimental conditions.

TABLE 2

Comparison of the Operated Groups for Differences in Curve Shapes and Curve Levels

	OC vs. HF	OC vs. LF	HF vs. LF
Mathematical functions	NS	NS	NS
Mathematical constants	NS	$p = .07$	$p = .05$

Note: Two-tailed test used.

With this in view, let

E_T = number of errors on a given occasion T (day or trial);

E_o = number of errors made on the first occasion (day or trial);

k = a constant proportional factor relating number of errors on a given occasion to the number of errors on the preceding occasion.

Now set

$$E_T = E_o k^{T-1}. \qquad [1]$$

This equation asserts that the number of errors that will be made on a given occasion will be equal to the number of errors on the immediately preceding occasion, multiplied by the constant of proportionality k.

It now remains to determine the value of k from the data secured under each experimental condition. Utilizing the method of least squares, it can be shown that the value of this parameter may be calculated from the equation

$$\log k = \frac{\sum_{T=1}^{n} Y_T(T-1) - c\sum_{T=1}^{n}(T-1)}{\sum_{T=1}^{n}(T-1)^2} \qquad [2]$$

where $Y_T = \log E_T$; $C = \log E_o$; and T = the ordinal number of the occasion (day or trial), and takes on the sequential values from 1 to n, inclusive. Utilizing equation 2, with E_T as the average number of errors made by a given experimental group on the T-th day (cf. Fig. 2), the values of k for the OC, HF, and LF groups were calculated. These values were found to be: OC = .600; HF = .606; LF = .691. Substituting the appropriate value of k in equation 1, we calculated the average number of errors to be expected from the rats in each group on a given day. These values are shown in Table 3, together with the values actually obtained (cf. Table 1). The fit for the OC group is fairly good; the other two groups show drops that are too sharp on the second and third days.

It is desirable to know whether these three values of k are significantly different. The problem is perhaps best treated by Fisher's method of orthogonal polynomials (1). The obtained values of E_T for each group were first translated to logarithms; Fisher's method was then used to calculate the slope of the straight line of best fit for each of the three groups. These slopes were found to be: OC = −.2129; HF = −.1846; LF = −.1293. Fisher's technique permits the calculation of the standard error of each value. In making the three possible comparisons, the only critical ratio approaching significance was that between the OC group and the LF group; this t was significant at approximately the 7 per cent level

TABLE 3

Average Errors per Day (E_T) for the Three Operated Groups, as Obtained and as Calculated by Formula

DAY	OC		HF		LF	
	CALCULATED	OBTAINED	CALCULATED	OBTAINED	CALCULATED	OBTAINED
1	12.8	12.8	13.7	13.7	14.	14.
2	7.7	7.6	8.2	5.6	9.7	6.8
3	4.6	4.3	5.0	4.0	6.7	5.4
4	2.8	2.1	3.0	3.4	4.6	4.7
5	1.7	2.1	1.8	2.1	3.2	3.8

Note: The ratios of the variance of estimate to the variance of the corresponding obtained E_T values are, respectively, .009, .094, .155 for the OC, HF, and LF groups.

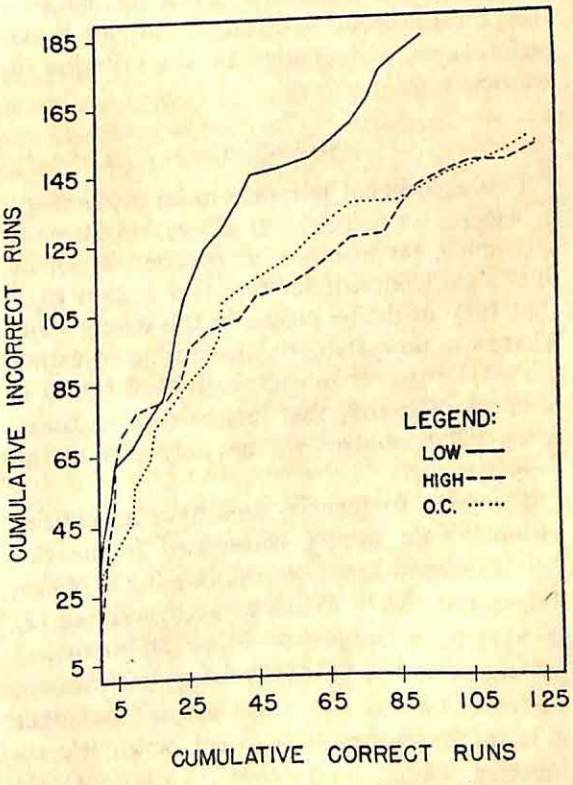

FIG. 3. Ratio of correct runs to incorrect runs

(two-tailed test). In making these comparisons, the error SS for the three groups were pooled, yielding 9 *df*. Since but five days were involved, the curves contain only five points, thus making the test very severe.

Perhaps the clearest summary of the findings for the three operated groups is given by Figure 3. The three graphs represent cumulative curves compiled according to a method described by Gulliksen (5). The method as here applied consists in determining the number of errorless runs and the number of incorrect runs made on each trial by all the animals in a group. These values were added to the total number of errorless runs and incorrect runs, respectively, made by the whole group of animals up to that point. This procedure is followed for each trial until the end, and yields number of cumulative errorless runs and number of cumulative nonerrorless runs as the two coordinate values. Since the method is best utilized when N is equal for the groups, randomized procedures were employed to reduce the size of two groups to that of the smallest of the three.

It will be seen from these graphs that while the OC and HF groups are hardly distinguishable, the LF group is distinctly inferior in its performance, as measured by the criterion of errorless runs.

DISCUSSION

This experiment purports to be exploratory in nature. As pointed out above, no attempt was made, for instance, at precise placement of the electrodes, if for no other reason than that they might be placed in the wrong spot! There was no systematic attempt at adjusting the level of power to each individual rat. It is obvious, of course, that factors such as these, when left uncontrolled, can only add to the error variance.

The pulse frequencies used have no ulterior rationale; we merely chose two frequencies that were quite far apart, thus hoping to obtain differential effects. While we are convinced (2) that impulse frequency is an all-important parameter in the neurophysiology of learning, we can at present only speculate as to whether it is in the nature of a direct or an inverse function. Thus, we note that the LF group did less well than the OC group, while the HF group was comparable to the OC animals. Does this mean that the imposed lower impulse frequency had an adverse effect, and the higher impulse frequency no effect at all? What would have occurred to the HF animals if we had used a repetition rate of 500/sec. instead of 300/sec.? Would they have performed even better than the OC rats? Perhaps the imposition of an extraneous stimulation on the rat's brain merely serves to worsen its performance when the stimulus repetition rate is below some value, whereas repetition rates above that value have no effect whatsoever at the power levels used. All of these and cognate problems require additional experimentation.

One aspect of the investigation that is perhaps quite unsatisfactory is the use of a maze. In an experiment where the emphasis is primarily analytical, the maze is an unnecessarily complex instrument, which can contribute more than its share to the error variance. In experiments presently being performed, simpler learning situations are being utilized.

Of methodological interest is the fact that the learning curves—and that of the OC group, in particular—could be described to a fair degree of approximation by the hypothesis that the rate of improvement is constant from trial to trial. This permits the possibility of determining the "learning rate" for any given stimulus frequency, and of investigating any relationship that may exist between these two variables.

SUMMARY

1. An experiment is described in which the cerebrum of the white rat is stimulated while the animal is in the process of learning a maze.

2. Two repetition rates of stimulation were used, and there is reason to believe that differential effects on maze learning were obtained, although the differences never exceeded the 5 per cent level of significance.

3. There is no reason to believe that the two stimulus repetition rates affected the shape of the learning curves, but only the constants in the learning-curve equation.

4. A method is described for calculating the "learning rate" involved in any given empirical learning curve.

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Received February 15, 1954.
Early publication.

THE EFFECT OF ELECTROCONVULSIVE SHOCK ON FIXATED BEHAVIOR IN THE RAT: II. THE EFFECT OF ECS SUPPLEMENTED BY GUIDANCE[1]

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Recently, Neet and Feldman (4) reported an attempt to modify abnormal behavior in the rat by using applications of electroconvulsive shocks (ECS). They found that a series of 10 or 25 ECS, administered one per day, was ineffective in causing rats to abandon conflict-induced, unadaptive, stereotyped behavior patterns on a Lashley jumping stand when more adaptive responses were available in a subsequent soluble problem situation. It was proposed that one possible reason for these negative results was that the effects of the shocks were masked by the difficulty of the testing situation.

Studies by Maier and his students (2, 3) indicated that if rats that had been placed in an insoluble problem situation on a Lashley jumping stand were forced to make adaptive responses during subsequent soluble problem situations, they were almost always able to abandon conflict-induced stereotypes and solve the problem. The rats were forced to make adaptive responses by the *E*'s placing his hand against the rat and nudging it toward the correct window while preventing a response to the incorrect window. This technique was designated by Maier as "guidance." Now, then, since ECS applications by themselves did not lead to remission of abnormal behavior patterns, in this study the animals, in addition to receiving ECS applications, were guided to the correct window on 50 per cent of the trials during a soluble problem to help insure mastery of the problem. Thus, the role of ECS as an aid to guidance could be observed, and a more sensitive measure of the effects of ECS is provided.

METHOD

Twenty-four male and 23 female mature albino rats were first trained in a modified Lashley jumping stand. The details of the training procedures are described by Neet and Feldman (4) and are only summarized here. At first, the animal was placed on the jumping platform close to the windows and induced to go through the windows to reach a feeding station on the other side. Gradually, the platform was moved back until the animals had to jump $8\frac{1}{2}$ in. through the closed windows.

After this training, the rats were confronted with an insoluble problem situation for 160 trials, 10 trials per day. The problem was insoluble because no matter what the rat did, it was punished 50 per cent of the time in random order. In other words, if the rat jumped persistently to the left or to the right, or to the bright or to the dark window, it was rewarded 50 per cent of the time and punished 50 per cent of the time. Rewarded responses consisted of going through an unlocked window and obtaining food on the platform behind the windows, while a punished response involved a bump on the nose and a fall to a net below. The rats soon showed resistance to jumping during this procedure, but a response was forced by energizing an electric grid on the jumping platform if they failed to respond within 30 sec.

After the insoluble problem stage, the animals were divided into a shock and a nonshock group on the basis of the types of responses they developed—left or right, or bright or dark—and the number of times that the response was practiced. The shock group then received one electroshock per day for ten consecutive days, using a modification of the Pittsburgh shock device (5), which administered a shock of 20 Ma. for 1 sec. The nonshock animals rested in their cages during this period.

All animals were then returned to the jumping

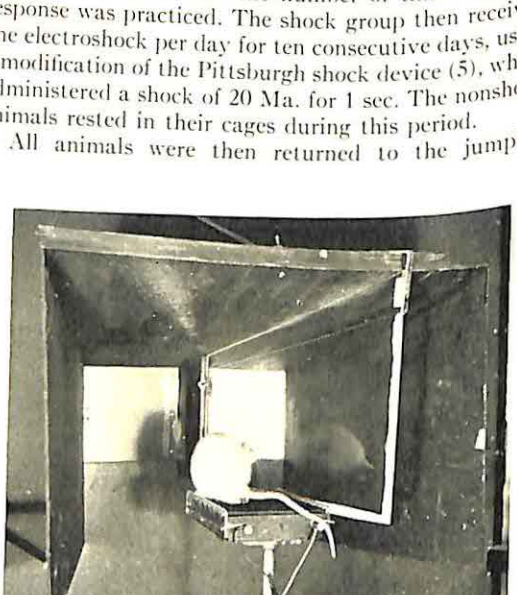

FIG. 1. The method of using the Plexiglas screen on guided trials. Here the rat is being forced to respond to the dark window, which is correct.

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[1] This research was supported by a research grant (MH-376) from the National Institute of Mental Health, National Institutes of Health, Public Health Service.

stand, where they were presented with a soluble problem. The dark window was the positive stimulus, unless the rat had developed a stereotyped response to that window during the nonsolution stage. In that case the bright window was correct. Also, on every other trial, the rats were guided to the correct window by placing beside the rat a transparent Plexiglas screen, which prevented a response to the incorrect window. An unpublished study by Feldman and Newman (1) showed that using a Plexiglas screen in this way had the same effect as manual guidance. Since this procedure was more standardized and obviated any differences that might exist between *E*s, it was the technique used in this study. Figure 1 illustrates the method of using the screen for guidance. This procedure continued until the animals abandoned the stereotyped responses acquired during the nonsolution stage and practiced the correct response on the nonguided trials for three consecutive days without making more than one error, or until they had a total of 200 free and guided trials.

RESULTS

In the nonshock group, it was found that all 23 rats were able to abandon their stereotyped responses and learn the new discrimination; but in the shock group, 1 animal out of 24 failed to solve the problem within the 200-trial criterion. The group differences obviously were not significant.

An analysis of the learning scores showed that the shocked animals learned in an average of 67 trials (including criterion trials), while the nonshocked animals learned in an average of 61 trials. This difference was not significant ($p = .16$).

Also, an analysis was made of the breaking scores. The breaking score is the number of that trial at which the rat first abandons its stereotyped response on a free trial during the soluble discrimination problem. Previous studies have shown that the magnitude of the breaking scores was directly related to the number of trials in which animals were subjected to conflict in an insoluble problem situation (4). Therefore, the breaking score can be considered as an extinction index of a conflict-induced response. It was reasoned, therefore, that if shock was an effective therapeutic device in re-establishing adaptive responses in animals that had been subjected to conflict, the breaking scores of shocked animals would be significantly lower than those of a nonshock group. The analysis showed that the mean breaking score of the shocked group was 26.5 trials, and that of the nonshocked group was 26 trials. This difference, of course, is nonsignificant.

CONCLUSIONS

The conclusions of this study are obvious. The use of ten electroconvulsive shocks under the conditions stated are without any effect in supplementing the guidance trials in establishing adaptive responses in rats that had been subject to a conflict situation. Possible reasons for these results are that we are dealing with a behavior manifestation that is invulnerable to shock treatments, that an insufficient number of shocks was administered, or that the guidance technique also was too effective and covered any possible effect the shock might have had. These results suggest additional studies in which the duration of the shock series would be increased, or the conflict-inducing situation would be shortened.

SUMMARY

Forty-seven albino rats were trained on a Lashley jumping apparatus and subjected to conflict in an insolvable problem situation. This produced stereotyped behavior in the rats. Approximately half the rats then received one electroconvulsive shock per day for ten consecutive days. The control rats rested. Both groups were then tested in a solvable discrimination problem in which the rats were guided to the correct response on 50 per cent of the trials. No significant differences were found between the shock and nonshock groups for the extinction rate of the conflict-induced responses, the number of rats that were able to solve the discrimination problem, or the number of trials required to solve the discrimination problem. It was concluded that a ten-day series of electroconvulsive shocks was ineffective in supplementing guidance procedures to induce extinction of conflict-induced stereotypes and the acquisition of adaptive responses in a subsequent solvable discrimination problem.

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Received September 28, 1953.

EFFECTS OF HYPOPHYSECTOMY ON BEHAVIOR IN RATS: I. PRELIMINARY SURVEY[1]

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Because of the limited scope of studies of the effects of hypophysectomy on innate behavior and learning in rats (1, 2, 3, 4, 5, 6), only the most tentative generalizations are warranted in respect to its effects. With a view to extending our knowledge in these areas, a series of studies on the behavioral effects of hypophysectomy in male rats was begun in the psychology laboratory at Stanford University in 1952.

What follows here is a preliminary survey of nesting and maze learning that had a twofold purpose: (*a*) to discover limits of durability of hypophysectomized rats to withstand the daily routines of thermal variation, food deprivation, and learning trials that entail a considerable output of energy; and (*b*) to ascertain the direction of change, if any, in nesting and maze learning after hypophysectomy of young males at the age of 40 days, when they are about midway between weaning and sexual maturity.

ANIMALS

Male albino rats of the Sprague-Dawley strain, hypophysectomized at the age of 40 days by the Hormone Assay Laboratories, Chicago, Illinois, were used. The intent of the operation was to remove both the anterior and posterior lobes completely without damage to the hypothalamus. A few of the animals failed to survive the combination of operation and transportation to our laboratory 48 hr. later. Twelve operates (E) and 10 normal controls (C) began the experiments. One of the E group died when 89 days old.

The diet of both groups consisted of a liberal offering of ground horse meat, wet mash made of the Steenbock mixture (8), Purina Dog Chow, and fresh oranges, carrots, and lettuce. Morton's salt cake was available in the cage. Two weeks after the operations, horse meat was deleted from the foregoing list. Weights were recorded on alternate days. Approximately seven days after the operations, all animals were examined in respect to length of tail, growth of hair, size of testes, distention of scrotum, and development of penis, particularly the glans and distal cartilage. Already, differences between operates and controls could be seen in all these areas, the most striking, however, being in body proportions and in size and position of the testes. Further details of the rate of differentiation of hypophysectomized and control rats must await comparisons of rats that are measured and autopsied on a day-to-day basis following the time of hypophysectomy. For the present, however, a few highlights will be given to indicate the major trends of differences.

Table 1 gives the mean weights of the E and C rats near the first and the last days of the experiment proper. Each entry is based on three weighings taken on alternate days and centered at CA 55 and 100 days. Prior to the first of these, all the animals had recovered from dehydration incurred in shipment, and between the first and second weighings neither food nor water deprivation had occurred. The asterisk indicates individuals that were not completely deprived of the anterior lobe. Figure 1 shows the disparity in size between an imperfectly operated male weighing 130 gm. (65 days after operation) and a normal control weighing 475 gm. His hair, for the most part, was very soft and fine as compared with that of the control. However, some coarse guard hairs were observed on the back, where they are most prominent in the control. This operated rat increased its operation weight by approximately 30 gm. during a period of 65 days. The size of the testes, their position in the scrotum, and the appearance of the penis led us to suspect that a remnant of the anterior lobe was present. Before being sacrificed he was placed with four young females similar to himself in size; one of these was in estrus. This one was impregnated within a few hours and two of the others within three days. Normal litters appeared from these inseminations. Autopsy of this male revealed sperm in the testes and *ductus deferens*, turgid seminal vesicles about half as large as those of a normal control, and normal-appearing coagulatory glands. A remnant of hypophysis in the *sella turcica*, about one-third the size of a pin head, proved on histological examination to be of the anterior lobe of the hypophysis.[2] Figure 2 contrasts the testes of this male with those of two males of the same age: one normal and the other completely hypophysectomized. The latter had testes about the size of a grain of wheat.

All the hypophysectomized rats of this study were autopsied approximately 75 days after their operations. In rats B, E, and F (see Table 1) minute remnants of the

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[1] This study was supported by a grant from the Scottish Rite Fund for Studies on Dementia Praecox, New York City, to which grateful acknowledgment is made.

[2] We are indebted to Dr. Hadley Kirkman, Director of the Anatomy Department, and his technician, Miss Marilyn E. Robbins, who inspected the heads of hypophysectomized rats for remnants of the hypophysis. They sectioned and identified all remnants found.

TABLE 1

Weight Changes of Hypophysectomized and Control Rats at 55 and 100 Days of Age (or 15 and 60 Days after Operation)

OPERATED			CONTROL		
Rat	Initial	Final	Rat	Initial	Final
A	109	113	1	206	328
B	113	120*	2	200	346
C	109	114*	3	212	344
D	121	125	4	194	330
E	111	127*	5	208	330
F	87	108*	6	206	328
G	103	115	7	182	280
H	109	115	8	156	260
I	115	122†	9	158	294
J	113	111	10	182	300
K	117	117			

* Small remnant of anterior lobe found.

† No remnant found; presence inferred on basis of growth of reproductive tract.

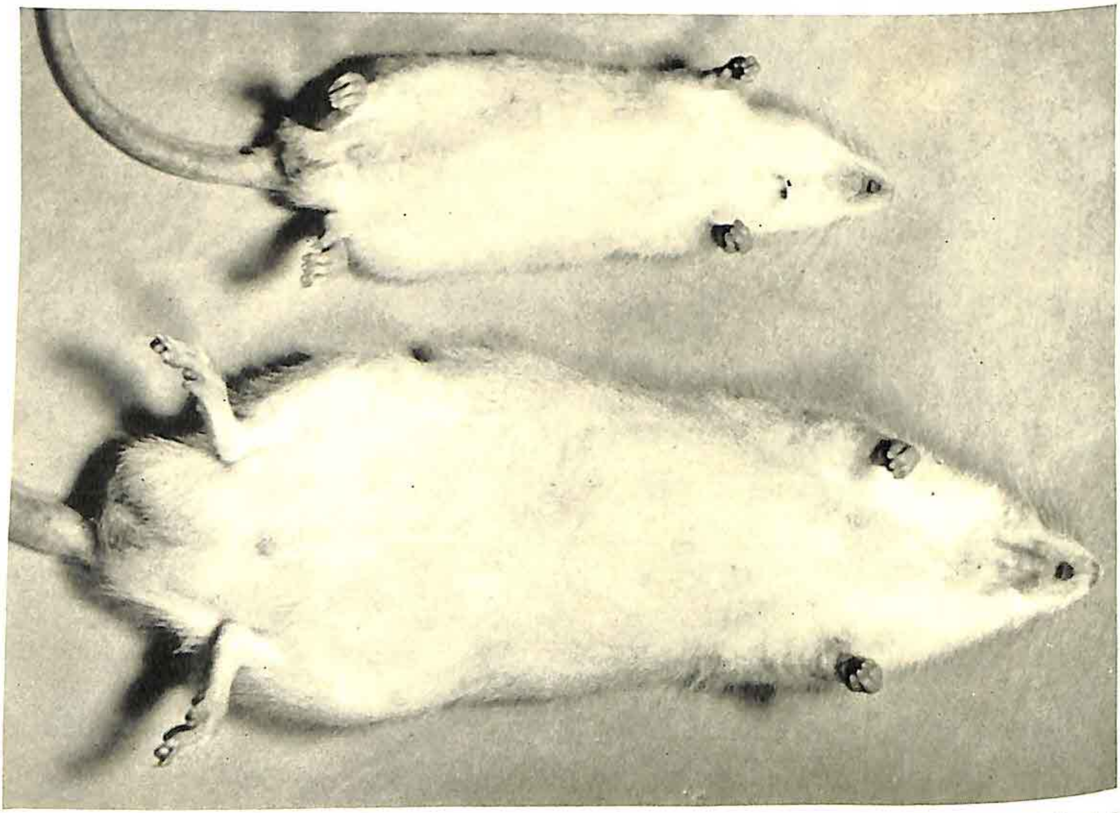

FIG. 1. An imperfectly hypophysectomized male and a control of the same age (CA 105 days; 65 days post operation).

anterior lobe were found. None was found in rat I, but it had sufficient growth of the reproductive system to justify suspicion that an undiscovered remnant was present. In all four, the testes were intermediate in size between those of the two operated animals shown in Figure 2. In all, a few sperm were found in the testes, the seminal vesicles were slightly enlarged, and the coagulatory glands contained a considerable amount of fluid. Also, the glans of the penis was better developed in them than in the operates which we believe were completely hypophysectomized. No breeding tests were made on any of the E group.

NESTING

Smith (6), in his pioneer studies of hypophysectomized rats, noted that they appear to suffer more from cold than their controls do. Bearing on the same point are studies by Richter (3), which show that hypophysectomized rats, when provided with thermal incentive and suitable materials, will build larger nests than normal animals.

Method

In the present survey we have used a relatively crude, naturalistic method to compare thermoregulatory behavior of the E and C groups. Each rat was assigned to a cage of the dimensions 12 in. by 18 in. by 24 in. In groups of four, the cages were enclosed in a large wooden box with a glass door. At the rear of the wooden box were holes for ventilation, and on top (at the front) was a small fan that drove a current of air into the box. The air was directed downward along the glass door rather than upon the individual cages. One-half inch of coarse wood shavings was placed on the

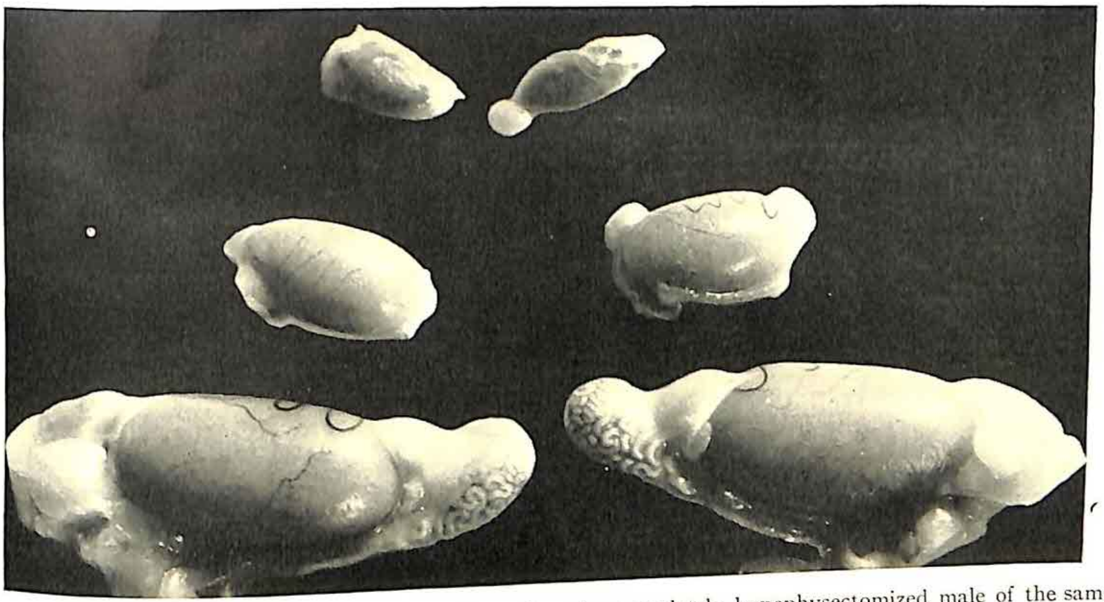

FIG. 2. Testes of the two males shown in Figure 1 and a completely hypophysectomized male of the same CA. The latter had testes similar in size to a grain of wheat; they contained no spermatozoa. The imperfectly hypophysectomized male sired three litters.

metal floor of each cage. Over this, 60 gm. of shredded newspaper were loosely strewn. The shavings and paper were the only available materials for nest construction. The paper, when heaped up properly, sufficed to cover a rat completely; the shavings, when swept toward the mound, buttressed the pile of paper. Hypophysectomized and control rats were housed randomly in the four-unit boxes, but the location of an individual's cage was never varied from start to end of the study.

Using the 0- to 5-point rating scale described by Walker and Stone (9), each of the present authors, working independently, appraised the nests. Daily ratings occurred between 7:30 and 8:00 A.M., while low temperatures prevailed in the laboratory, and each nest probably represented the best construction achieved by an animal during the night. For the first six days, *E*s did not touch the nests, but after the sixth day's ratings all paper was removed and replaced by new paper, spread over the floor as at the outset. Thus, ratings for the first and seventh days were based on fabrications of only one night, those of succeeding periods, on nests that had undergone varying amounts of reconstruction from day to day. The night temperatures varied from 48° to 64°F. during the ten-day period; daytime range was from 68° to 85°F. until 4:00 P.M., when the heat was turned off, which allowed the room to cool gradually.

Results

Figure 3 graphically represents the means of ratings for the ten-day period. On the whole, the nests of hypophysectomized rats were judged to be better thermoregulatory devices than those of the controls. More of the E group used all available paper and enveloped themselves (rating, 4) than was the case with the controls; also, fewer of them made open-top nests, for which ratings of 3 or less were given. Neither group made much use of shavings. A t test, based on records for ten consecutive nights, indicates that the difference between means, favoring group E, is clearly significant ($p < .001$).

Since the nests were constructed *de novo* only on the first and the seventh nights, one cannot adequately compare the two groups in regard to persistence of renestbuilding. It may be said, however, that some renestbuilding. It may be said, however, that some re-

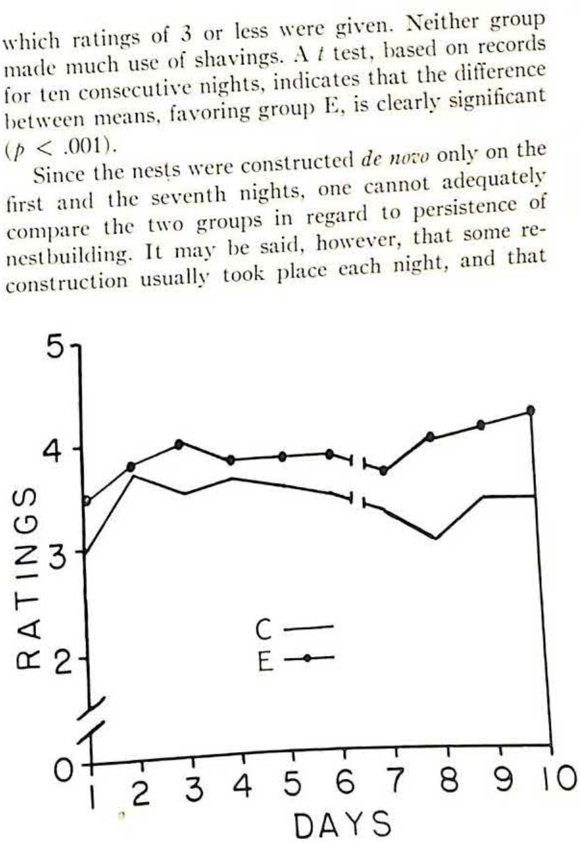

FIG. 3. Nests constructed by hypophysectomized and control rats (beginning at CA 58 days; 18 days post operation). Group means are based on averages of the ratings by two independent observers.

the operates as a group did more of it than the controls (note rise in graph of group E).

MAZE LEARNING

At the end of the nesting study, we started preliminary training for the water mazes. This consisted of three swims daily for three days down a 10-ft. straight alley with metal walls 14 in. high and about 6 in. above the water line. The temperature of the water, as well as that of the room, was maintained at about 75°F. Retracings were permitted, but the rat could not leave the alley except at the distal ramp. About 5 or 6 min. elapsed between trials. While waiting the *S*s were kept in a warm cage.

Maze 1

The floor plan of this four-unit swimming maze is shown in Figure 4. Each unit is 38 in. long (outside measurement) and an alley is 5 in. wide. Gates limit retracings to a single unit. Water was maintained at a depth of 8 in. and at a temperature of about 75°F. Each rat received two trials daily, with an interval of from 10 to 15 min. between swims. While waiting they were kept in warm containers. The trends of learning by the E and C groups are presented in terms of forward-going errors for 26 trials. There was little difference between the means for the first ten trials, but thereafter improvement by the control group exceeded that of the hypophysectomized group. This reflected a greater tendency on the part of some of the E group to stereotype their wrong choices. Whether stereotypy of errors among the E group arises from some unfavorable emotional aspect of their motivation, rather than from a true difference in learning capacity, is a question that cannot be answered from the data now available. This factor of "fixation" also accounts for the E group's having a lower mean for perfect trials (5.3 for E vs. 9.6 for C). This difference is consistent with the trend of error scores, but is barely short of significance at the .05 level. The group difference for the totals of forward-going errors, tested by *t*, is significant at the .05 level.

Maze 2

This swimming maze (see Fig. 4) combines characteristics of the T and the Warden U maze. Its dimensions are approximately the same as those of Maze 1. It was placed at the end of the water tank directly across from Maze 1. Thus, some extramaze objects within the animal's range of vision would appear at new places when it began the trials on Maze 2. The door limited retracings to one unit.

One day after the last trial on Maze 1, all animals were started on Maze 2 without any preliminary trials. We desired to introduce a sudden change of maze patterns in which both positive and negative transfer factors would operate. Three trials daily were given. Again, approximately 10 to 15 min. elapsed between

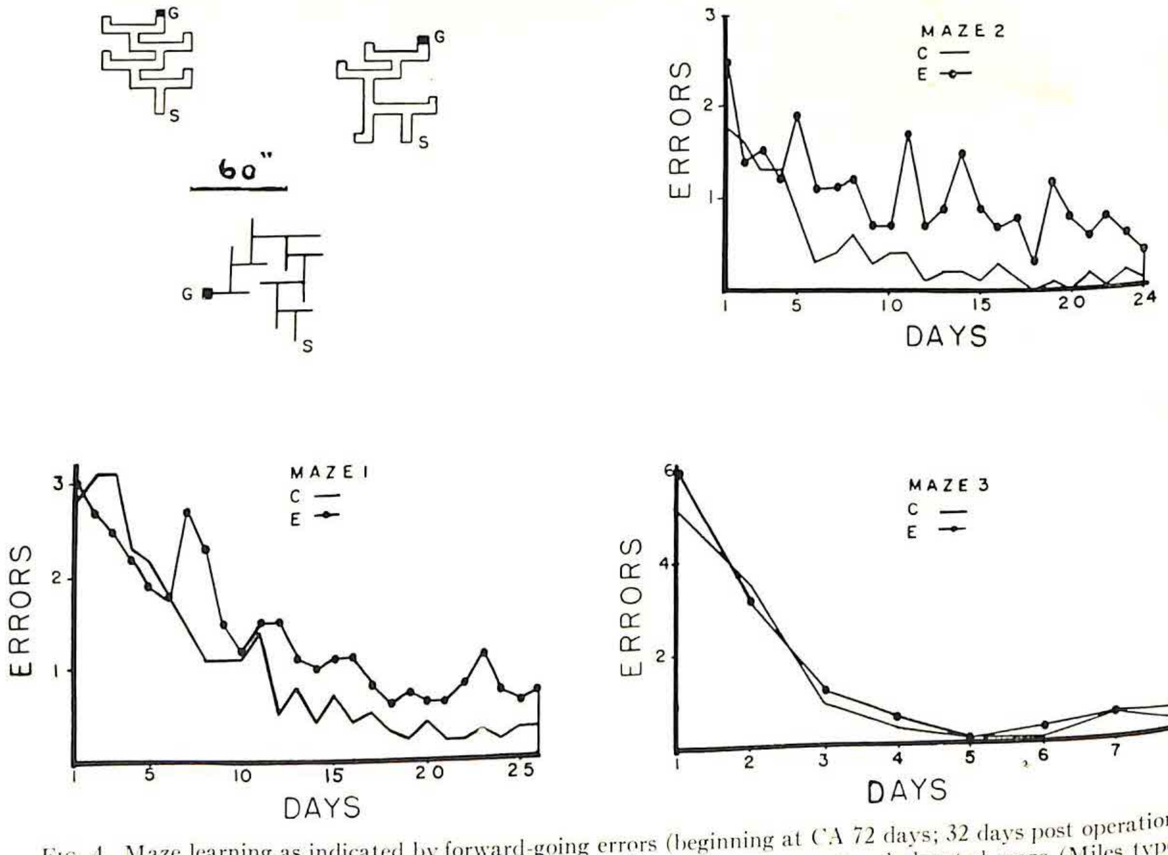

FIG. 4. Maze learning as indicated by forward-going errors (beginning at CA 72 days; 32 days post operation). Mazes 1 and 2 are 4-choice swimming mazes; Maze 3, an 11-choice, narrow-tread elevated maze (Miles type).

individual trials. The graphs of Figure 4 are based on forward-going errors. As is evident, the rate of improvement by the control group was superior to that of the hypophysectomized rats, beginning with the second day. The mean number of errors for 24 trials was 25.2 for E and 11.0 for C. This difference is significant at the .001 level. Group E made slightly more retracings than C, but the difference was not significant. The mean number of perfect runs of the controls is significantly greater ($p < .01$) than that of the E group (12.8 vs. 6.9).

As with Maze 1, the performance of the E group was characterized by more of the persistent, stereotyped errors. Also, by the third trial each day, most of them showed more unmistakable evidence of fatigue by their manner of swimming than was shown by the controls. It may be presumed that the three swims on this maze closely approached their limit of physical endurance.

Maze 3

An elevated, narrow-tread maze (Miles type) was introduced to provide a situation in which a difference in strength and physical vigor would not be disadvantageous to the operated rats. This maze also permits an animal to perceive in advance of a choice point the fundamental differences between an arm of the maze that ends in "thin air" and one that forms a continuous pathway. By attention to this detail the rat virtually converts the fixed pattern of the maze into a serial discrimination apparatus. Ordinarily, the mastery of such mazes has been found to be more rapid than mastery of alley mazes of similar pattern. For preliminary training, two units (one 3 and one 6 ft. long) were set end to end in front of the open door of the home cage from which the occupants had been temporarily removed. In this were water and the following foods: wet mash, Purina pellets, orange, lettuce, carrot, and sunflower seeds. All water and food were removed from the home cage 16 hr. before training began. Under this condition the rats partook of water or food immediately on arrival at the home cage. Each animal had five trials daily for three days. On the third day, the short unit was set at right angles to the long one and about 10 in. from the distal end. This was done to acquaint the rats with an arm that ends in "thin air" in contrast with that which continues to the goal. Orientation of the home cage in the laboratory was varied from trial to trial so as to minimize attention to specific objects in the room that might later on afford directional cues for running the maze.

On Maze 3 each animal had one trial daily. If it appeared probable that the rat would not reach the home cage on its first trial because of persistent retracing, a barrier was placed on the runway, where needed, to check retracing at this place and thus to encourage advancement toward the goal. Beyond trial 1 this barrier was not used. Figure 4 represents the forward-going error data for eight trials, the limit of this experiment. No significant difference in rate of error elimination was found. The controls were somewhat more sure-footed than the operated animals, but as a rule they did not complete their runs in shorter time. Both groups, on arrival at the home cage, sampled water and food. This, together with promptness of starting and absence of exploratory excursions during the runs, suggests that motivating conditions were effective for both groups. Whether or not there was equality, however, cannot be inferred from the evidence at hand. Noteworthy, and possibly significant, was the absence of stereotypy of erroneous turns on the part of the hypophysectomized rats.

COMMENTS AND RECOMMENDATIONS

The *E*s were happily surprised to find that the hypophysectomized rats in individual cages were able to withstand night temperatures ranging from 48° to 64° F. with the aid of nests that they constructed from the raw materials provided them. The results lend support to the hypothesis of Richter (3) that greater nesting on the part of the hypophysectomized rats is a compensatory adjustment instigated by greater need of heat because of their lower metabolic rate. This hypothesis would be strengthened, however, if it were known that no nesting occurs when temperatures pass above a specific range (e.g., 90° F.) and that cessation on the part of the controls occurs at a lower temperature than with the operated rats. Also, it would be strengthened if in individual tests of thermal preference, in a long, narrow cage having a thermal gradient ranging from about 60° to 100° F., the hypophysectomized rats tended to spend more time or lingered in and came to rest nearer the upper limit than the controls did. These and still other tests must be made before one can confidently endorse the conclusion that superior nesting on the part of the hypophysectomized rats denotes the working of an innate homeostatic mechanism for heat regulation. At present, nevertheless, we incline toward this viewpoint.

Although the results from our three mazes are not in perfect accord, the following statements regarding hypophysectomy of 40-day rats appear to be warranted: (*a*) learning rate is not improved by this operation; (*b*) when performance is impaired, the amount is small and highly variable from individual to individual; and (*c*) greater fatigue or unpleasantness associated with maximal physical exertion may have instigated and "fixated" more errors on the part of the operated rats, thereby causing inferiority that does not truly reflect their ability to learn under more favorable circumstances.

Data from previous publications on hypophysectomized rats do not warrant dissent from the foregoing statements. Burnham and Leonard (2) reported that the mean for reverse learning of a simple black-white discrimination by three males, beginning 10 days after hypophysectomy at age 40 days, was about the same as that for the same number of controls and pseudo-operates. In our opinion, no conclusion can be drawn from their report on seven females, tested six months after hypophysectomy (age unspecified), because of the absence of appropriate control data.

Further studies of learning, following total and partial hypophysectomy, are needed. Inspection of our records of four incompletely hypophysectomized males did not reveal any differences between them and the other operates in either the nesting or learning situations. From so few cases, however, no conclusions are warranted. Further study is justified on the ground that with partial hypophysectomy one has to keep in mind the sexual component of motivation that is absent or minimized in the others. This sexual component may be accompanied by greater strength and endurance. Noteworthy also in this connection is the fact that no study of learning has been reported on rats with only the anterior or the posterior lobe alone removed. The standard operation removes both lobes. In the living animal a diagnosis of total versus partial hypophysectomy usually rests on signs that pertain only to functions of the anterior lobe. Possibly, remnants of the posterior, as well as the anterior, lobe may play a significant role in the motivation of learning behavior in certain situations.

Other variables in need of study pertain to the age of hypophysectomy and length of interval between operation and time of testing. Introduction of these variables can be justified on theoretical if not on experimental evidence. Possibly, to cause learning impairment, an operation must be performed prior to the time cell division in the cerebral cortex has ceased, i.e., before 22 days of postnatal life. Also, it is possible that several months should intervene between operation and the time of testing so that secondary disturbances that may influence cortical functions will become maximally effective.

Several types of learning beyond those herein used should be investigated. From our survey it is evident that tasks requiring a considerable expenditure of energy may be employed. Our hypophysectomized rats were very active. Their alertness resembled that of normal rats 30 to 70 days old. We believe that hunger and thirst may be employed in motivation if recourse to long periods of deprivation (20 to 30 hr.) is avoided. Our animals appeared to be well motivated in the water maze, with temperature at 75°F. No doubt this kind of motivation can be adapted readily to discrimination learning, detour problems, delayed reaction, reasoning, etc. In short, our survey suggests that many types of learning problems are both feasible and desirable.

SUMMARY AND CONCLUSIONS

The results of this survey would seem to support the following statements:

1. Male rats that are hypophysectomized when about midway between weaning and sexual maturity build superior nests, on the average, than do controls of the same age at temperature ranging from 48° to 64° F. This supports Richter's conclusion that the behavior is a compensatory adaptation prompted by their greater need of supplemental heat because of a lower metabolic rate.

2. The hypophysectomized rats as a group were slightly inferior to their controls in learning two swimming mazes, but not significantly different from the controls in learning a relatively simple elevated maze. Inferiority on the water mazes arises from greater "fixation" of errors by the hypophysectomized rats. Still unanswered is the question as to whether this arises from some adverse emotional factor rather than from a true inferiority in learning ability.

3. The present survey clearly shows that hypophysectomized rats are sufficiently active and hardy to undergo most of the laboratory tests ordinarily imposed upon normal rats in studies of innate responses, drive, learning, discrimination, or the so-called higher levels of cerebral functioning.

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Received February 12, 1954.
Early publication.

GASTRIC FACTORS CONTROLLING WATER- AND SALT-SOLUTION-DRINKING

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In the search for physiological mechanisms regulating thirst and specific hungers, much emphasis has been placed on the role played by sensory impulses arising from the mouth and throat. While there are some data to support this emphasis, it is also clear that important contributions to the control of these types of motivation arise in other parts of the body: the stomach, the blood, and the central nervous system, to name the most obvious ones.

The present investigation is concerned with the role of events originating in the gastric tract in the management of water drinking and the drinking of salt solutions. Some direct behavioral studies already indicate that water drinking may be inhibited by the mere presence of water in the stomach (2). Other more physiologically oriented data suggest that the relationship of drinking behavior to different concentrations of salt solution may be governed by variations in the capacity of the gastric tract to handle these concentrations. Experiments on the rate of absorption of various salt solutions placed directly in the duodenum, for example, show that maximum absorption occurs with approximately isotonic solutions, and falls off as the concentration of solution is both increased and decreased (5). This absorption curve very strikingly resembles the preference-aversion curve of the normal animal for sodium chloride, and suggests the possibility that the rate of absorption of solutions from the duodenum might have something to do with preference and aversion.

Perhaps even more significant is the fact that the ability of the stomach to dispose of solutions is also determined by the concentrations of such solutions (3). Normally, the stomach operates to render solutions isotonic (0.9 per cent NaCl) before passing them on to the duodenum. Although the stomach does not perform this function with perfect efficiency, it does close the pyloric sphincter when stimulated by strong solutions. Furthermore, if any hypertonic solutions do escape into the duodenum, they may be squirted back into the stomach by a reversed peristaltic action.

Finally, the possibility that some action of solutions on the gastric tract might be important in drinking behavior was also suggested by the shape of curves showing the rate of intake as a function of time (8). In general, it was found that the rate of drinking of all solutions is essentially the same for about five minutes. Then, in the case of hypertonic solutions, drinking abruptly ceases. In the light of the physiological data, it is a reasonable hypothesis that it is the gastric effects of these strong solutions that inhibit drinking.

In order to check this point, it was necessary to get various solutions directly into the stomach and circumvent the stimulation of taste and other mouth receptors. This end was achieved by means of a stomach-tubing technique described below. Then the experimental design simply became to measure the rate and amount of drinking of water and of salt solutions after loading the stomach with water and various salt solutions.

METHODS

Animals

Thirty-six adult male rats, descendants of the Lashley strain, were used in the experiments reported here. Twelve rats were used to obtain the basic preference-aversion function. Ten were used in the first stomach-loading experiment, six were used in the last two loading experiments, and eight were used in a preliminary study of drinking by animals prepared with esophageal fistulas.

Measurement of Drinking

All measures of water and salt solution intake were obtained by the single-stimulus method described previously by Weiner and Stellar (8). Each drinking test was introduced by 16 hr. of water deprivation. The test itself lasted 1 hr., during which time the animal had no food but was offered a single graduated drinking cylinder containing water or some salt solution. Then, after a 2-hr. rest without food or water, the rats were given tap water and Purina Laboratory Chow pellets for a 5-hr. maintenance period. At the end of the maintenance period, the water was removed, and the rats were left with food overnight for the next 16-hr. water deprivation.

In all cases, the fluid intake during the 1-hr. testing period and the 5-hr. maintenance period was recorded. Wherever necessary, drinking during the 1-hr. testing period was recorded at 5-min. intervals to give a measure of the rate of drinking.

Stomach Tubing

A No. 8, Robinson-type, French rubber catheter was used to introduce solutions directly into the stomach. The receiving end of the tube was attached to a hypodermic syringe loaded with some solution. The tapered delivery end was then dipped in mineral oil and removed gently to maintain a large drop of oil on the end. The rat was prepared for tubing by hooking its upper teeth over a rigid metal loop attached to a ring stand and pulling down on the lower teeth with another metal loop. With the mouth gently but firmly held open, the tube was introduced directly to the back of the tongue. When stimulated by the drop of oil, the rat swallowed and the tube was inserted. Its passage into the stomach was facilitated by the mineral oil and the swallowing reflex. Care was taken to be certain that the tube had gone down far enough to be in the stomach before solution was passed.

Two persons tubed the rats in this study, but one-man tubing can be accomplished by mounting the hypodermic syringe in a ring-stand clamp and using a foot-pedal device to pull down on the lower teeth. In fact, after rats are fully habituated to tubing, it is necessary only to hook the upper teeth and insert the tube through the side of the mouth, behind the teeth.

Control for Tubing

Six of the rats used in the first loading experiment were used to check out the effects of tubing on water drinking. On successive days, they were tested after no tubing, passing a tube but not administering fluid (dry tube), administering 3 cc. of water through the tube, and administering 3 cc. of 3 per cent NaCl.

Treatments

In the rest of the investigation, drinking was studied as a function of five treatments: (*a*) concentration of the solution drunk; (*b*) concentration of the solution loaded into the stomach, and concentration of the solution drunk; (*c*) volume and concentration of the solution loaded into the stomach, and concentration of the solution drunk; (*d*) delay between loading and drinking, volume and concentration of the solution loaded into the stomach, and concentration of the solution drunk; (*e*) concentration of the solution drunk minus any subsequent gastric effects (animals with esophageal fistulas).

The concentrations, volumes, and delays between loading and drinking are given below with the results.

Esophageal Fistulas

In this preliminary study, four rats were used as acute fistulated preparations, and four were used as controls. The operations consisted simply of exposing the trachea and freeing the underlying esophagus for about 2 cm. Then the esophagus was tied off with surgical silk as close as possible to the sternum and severed just above the knot. The free end of the upper esophagus was secured by two long loops of surgical silk passed through the cut opening, through the lining and wall of the esophagus, and out the side of the esophagus about 2 mm. above the cut end. The neck was then sutured except for a small opening in the mid-line just above the level of the thyroid gland. By means of the two loops of surgical silk, the esophagus was pulled gently through this external opening and attached to the skin by four or five separate sutures.

The animals used in this part of the investigation had been on the single-stimulus regime just prior to operation and could be tested with different solutions on the morning following operation. Four 1-hr. tests were run each postoperative day at intervals of 2 hr. Then at night, the animals were maintained by injection of 10 cc. of 5 per cent glucose intraperitoneally and 5 cc. subcutaneously. Following injection, they were left overnight with two graduated cylinders, one containing water and the other a salt solution.

The four control animals were used to check only one point—the effect of thirst on the drinking of 1.5 per cent NaCl. They were deprived of all food and fluid and maintained by nightly injections of glucose. At the end of four days, they were all tested for 1 hr. with a 1.5 per cent NaCl solution.

RESULTS AND DISCUSSION

Concentration of Solution Drunk

The mean fluid intake of 12 rats, plotted against the log of molar concentration of NaCl, yields a typical preference-aversion function. The ascending or preference limb of the function is positively accelerated and reaches a maximum between 0.7 per cent and 0.8 per cent NaCl. The descending or aversion limb is a very slightly decelerated function, nearly reaching a zero point at about 4.0 per cent

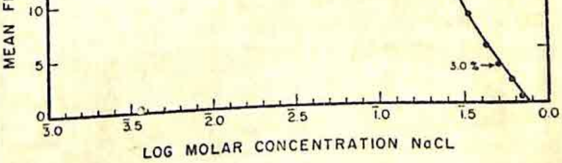

FIG. 1. The preference-aversion function for sodium chloride, showing the intake of water and various concentrations of salt solution

NaCl. Since a log scale of concentration is used, mean intake of water or zero concentration of salt is shown as a horizontal line. Assuming from previous experiments (1, 6) that the normal rat drinks the same amount of 0.01 per cent NaCl as it does of water, the ascending limb is made asymptotic to the water line at this concentration on the log scale. The final point to note about the preference-aversion function is that the descending limb intersects the water line at approximately 1.5 per cent NaCl, yielding an indifference point.

Control for Tubing

The process of passing a stomach tube into an animal will produce a slight depression of subsequent drinking, but not enough to mask the effects of loading different solutions into the stomach. Thus, in the control tests run here, six rats averaged 11 cc. of water in 1 hr. when not tubed, 8.5 cc. following passing a dry tube, but only 6.0 cc. when loaded with 3 cc. of water. When 3 cc. of 3 per cent NaCl were introduced, the rats drank slightly over 13 cc. in the one-hour period.

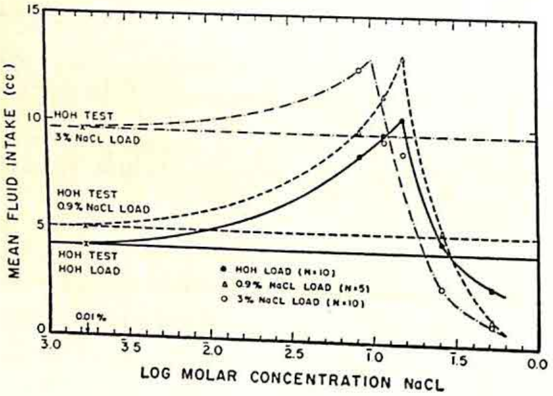

FIG. 2. The effect of 3-cc. loads of water, 0.9 per cent NaCl, and 3 per cent NaCl tubed directly into the stomach on the intake of water and various concentrations of salt solution

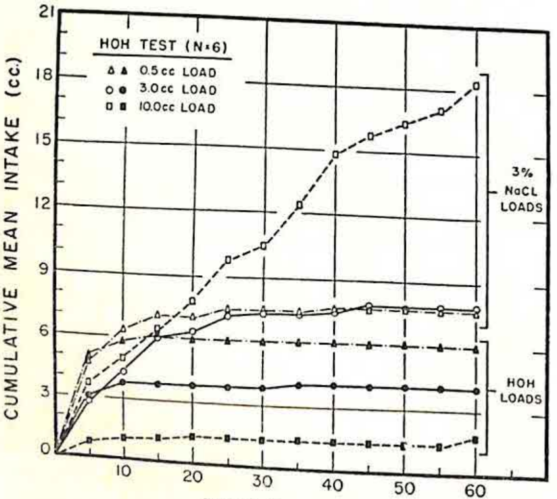

FIG. 3. The effect of water and 3 per cent NaCl loads of different volumes introduced directly into the stomach on the rate and total intake of water

Concentration of Loads

The results of this part of the experiment show that 3-cc. loads of different concentrations affect the drinking of water and various salt solutions differently. Taking into account all the solutions the animals were offered (water and 0.5, 0.7, 0.9, 1.5, and 3 per cent NaCl), one can see from Figure 2 that the 3 per cent NaCl load increases the intake of water and hypotonic salt solutions and depresses the intake of hypertonic solutions. Conversely, the water load depresses the intake of water and hypotonic salt solutions and increases the amount ingested of the hypertonic solutions. The 0.9 per cent NaCl load has an intermediate effect on the drinking of hypotonic and hypertonic solutions; but it produces more drinking of isotonic solutions than either the water or the 3 per cent load.

Put another way, the 3 per cent NaCl load shifts the maximum of the preference-aversion function toward the low concentrations, while the water load tends to shift it toward the high concentrations. This interpretation is shown in the free-hand fit of the data points shown in Figure 2. Other interpretations of these data may be possible, but the fits used here were based on two independent considerations: (*a*) the general shape of the preference-aversion function shown in Figure 1, and (*b*) making all the curves asymptotic to their water lines at the preference "threshold" concentration of 0.01 per cent on the log scale.

Volume of Load

Three noteworthy results came from loading the rats with 0.5-, 3.0-, and 10.0-cc. volumes of different solutions. The first is that the 0.5-cc. loads of various concentrations (water, 0.9 per cent NaCl, and 3 per cent NaCl) produced the same relative effects on the preference-aversion function as did the 3.0-cc. loads. The effects on water drinking are shown in Figure 3, but the

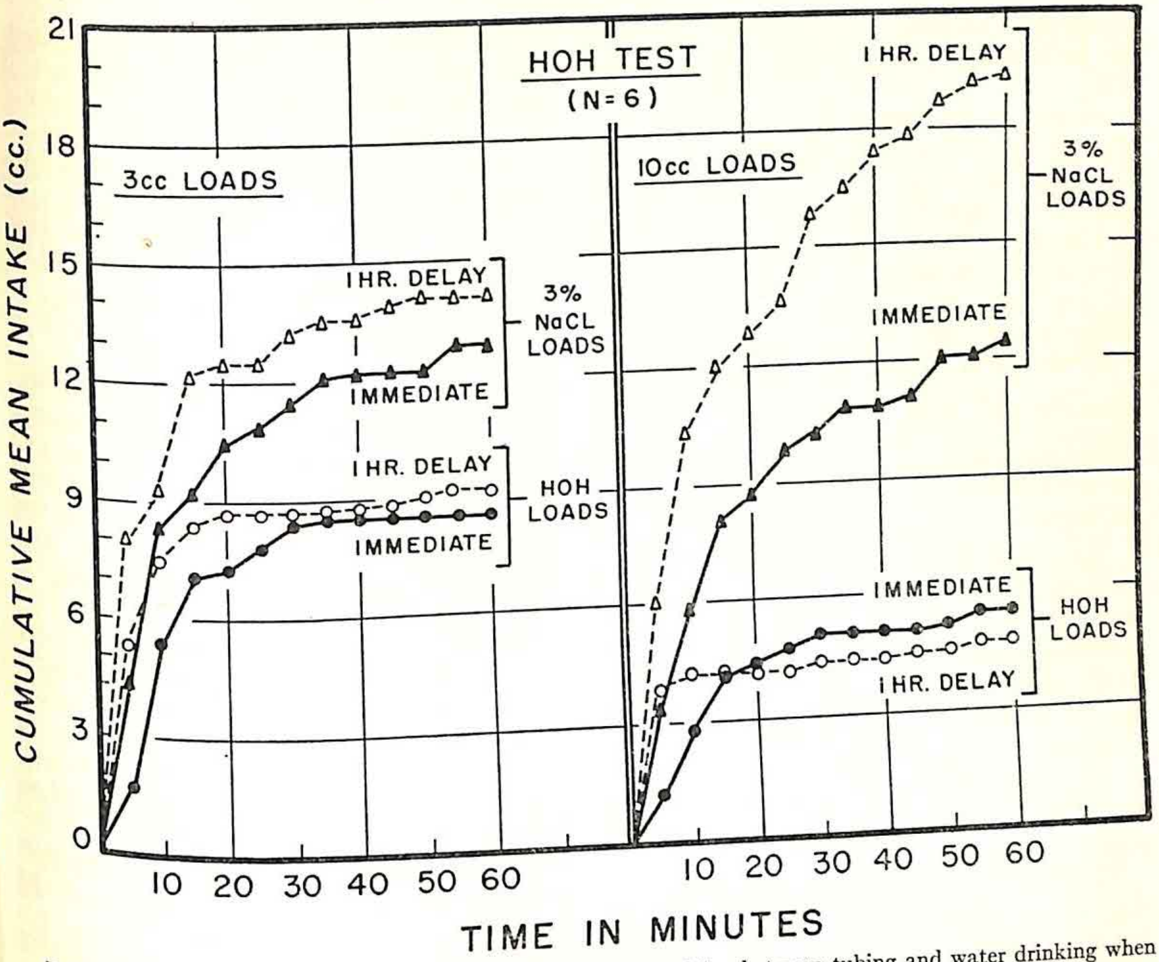

FIG. 4. The effect of a 20-sec. delay (immediate) and a 1-hr. delay between tubing and water drinking when 3-cc. and 10-cc. loads of water and 3 per cent NaCl are introduced directly into the stomach

same relative kinds of effects were obtained when the rats drank 0.9 per cent, 1.5 per cent, and 3.0 per cent NaCl. Although the effects of the 0.5-cc. loads are not usually as marked as those of the 3.0-cc. loads, it is clear that the mechanism controlling drinking behavior is sensitive to very small amounts of salt solution placed directly in the stomach.

The second point is that the 10.0-cc. loads in general tended to depress drinking to very low levels, regardless of the concentration loaded or the concentration drunk. Apparently, large volumes of fluid in the stomach will inhibit drinking even when solutions are introduced that might otherwise increase drinking. The third point is the one exception to this rule. When 10.0 cc. of 3 per cent NaCl was administered and the rats were allowed to drink water, they averaged over 18 cc. in their water intake for the one-hour period (Fig. 3). In this case, the thirst produced by the large volume of strong salt dramatically overcame the depressing effects of volume alone. So volume may tend to depress drinking, but it is not necessarily a limiting condition.

Delay between Loading and Drinking

Only one definite effect of varying the delay between loading and drinking shows up in this study. The first 10 to 15 min. of drinking after the 20-sec. delay (immediate) is always depressed when compared to the initial drinking following a 1-hr. delay. Figure 4 shows this effect only in the case of water drinking, but the same thing shows up when the rats are tested with 0.9, 1.5, and 3.0 per cent NaCl. That this depression of drinking depends upon the volume of fluid still in the stomach at the time of drinking is suggested by the fact that the initial depression of drinking is much greater with the 10.0-cc. loads than it is with the 3-cc. loads. Apparently then, there is some immediate depressing effect of a load introduced into the stomach that dissipates with time.

Despite these differences between the immediate and 1-hr. delay conditions, different solutions still produce their characteristic effects on drinking, regardless of which delay is imposed. Within 5 min. after the start of drinking, for example, 3 per cent NaCl loads produce more drinking than comparable water loads, whether the delay is an hour or 20 sec. (Fig. 4). So it appears that the various loads can produce their characteristic effects on drinking almost immediately, but yet these effects may persist for at least an hour.

Elimination of Gastric Factors

Two clear points come out of the study of animals prepared with esophageal fistulas. In the first place, when these animals were tested with water and with 0.7, 1.5, and 3.0 per cent NaCl, they showed the ascending and descending preference-aversion function. Thus, it seems clear that gastric factors are not essential for the basic form of the function. The taste mechanism alone can yield the preference-aversion curve.

The second point is that the fistulated animals drink much more of the hypertonic solutions than do normal controls. This point is brought out most clearly when the fistulated animals are compared with the unoperated controls in their ingestion of 1.5 per cent NaCl after both have suffered four days of water deprivation. The unoperated animals averaged 4 cc. of 1.5 per cent NaCl in a 1-hr. period, while the fistulated animals drank 29 cc. during the same period. Presumably, some effect produced by the hypertonic salt solution after it entered the stomachs of the normal rats inhibited drinking.

Interpretation

Taken together, the results of these experiments reveal a number of important points about water drinking and the drinking of salt solutions. First, taste and mouth factors alone can determine the ascending and descending form of the preference-aversion function for sodium chloride. Second, some events originating in the gastric tract inhibit the drinking of hypertonic solutions and account partially for the descending limb of the preference-aversion curve. These gastric factors may be set into operation by as little as 0.5 cc. of solution, and may take effect within 5 min. after ingestion. Yet the effect may last for as long as an hour.

What the gastric factor controlling drinking behavior may be is suggested by the experiments of McCleary (4). Working with sugar solutions, he found many of the effects shown in these experiments. He was further able to suggest, however, that hypertonic solutions introduced into the stomach produce their effects on drinking by pulling water into the stomach by means of osmotic pressure, thereby dehydrating the animal. As a matter of fact, he showed that the stomach need not be involved in the dehydration mechanism, for hypertonic solutions introduced directly into the blood stream have the same effects as hypertonic solutions introduced into the stomach. Not only that, but dehydrating animals by water deprivation will have the same effect on the preference-aversion curve as will hypertonic solutions introduced into the stomach—i.e., elevating the drinking of water and hypotonic solutions, and depressing the drinking of hypertonic solutions.[1]

Despite the fact that the dehydration mechanism can be brought into play without involving the stomach directly, it is quite clear that the stomach normally operates in the control of the drinking of the normal animal. For one thing, the ability of fistulated animals to drink large quantities of hypertonic solution when severely dehydrated points to the importance of the stomach in the inhibition of drinking hypertonic solutions by the intact animal under the same circumstances. Second, the major dehydrating effects of the hypertonic solutions an animal drinks must be produced by the ability of these solutions to pull water into the stomach, for their effects occur too soon for them to depend upon absorption into the blood stream from the duodenum. Third, if hypertonic solutions do actually pull water into the stomach, they not only dehydrate the animal, but they also may stretch the stomach enormously. In fact, direct observation of the exposed stomach of an anesthetized animal tubed with hypertonic solution shows clearly the rapid swelling of the stomach. Thus, some of the inhibiting effects of hypertonic solutions may be attributable to the depressing effects of large volumes of fluid in the stomach. The volume of fluid in the stomach cannot always be a limiting condition in how much an animal drinks, however, for hypertonic solutions elevate the drinking of both water and hypotonic solutions at the same time that they depress the drinking of hypertonic solutions. So dehydration must still play a unique and powerful role in the regulation of drinking behavior.

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[1] Sussman, K. E., & McCleary, R. A. Personal communication.

The picture is complicated, but it is clear that drinking behavior is under multifactor control. And we now have some idea of what these factors must be: taste, gastric distension, and dehydration normally produced by the effect of hypertonic solutions on the stomach, or otherwise produced. Thus, when the normal rat is tested with water and an increasing series of concentrations of salt or other solutions, its behavior must be regulated somewhat as follows: Most of the drinking of water must be determined by dehydration. With an increasing concentration series up to the isotonic point at least, dehydration plays some role, but taste is the dominant factor such that the stronger the taste stimulation, the more the drinking. With an increasing series of hypertonic solutions, there may be some negative taste or other sensory effect in the mouth (pain?) that contributes to the progressive inhibition of drinking. In addition, however, the effects of these hypertonic solutions on increasing the volume of fluid in the stomach, and more particularly, on producing dehydration, also contribute to the progressive depression of drinking.

Presumably, the contributions of these many factors are integrated in the central nervous system, since it is here that the response of the animal must be controlled. The best hypothesis we have at present is that such central nervous centers must lie in the hypothalamus (7). This possibility is now being checked by direct experiment.

SUMMARY

The role of gastric factors in the control of water drinking and the drinking of salt solutions has been studied experimentally by a stomach-tubing technique that permits the direct introduction of solutions into the stomach of the rat, without involvement of taste and other mouth receptors. Five experimental treatments were imposed on the 36 animals used in this investigation: (*a*) variation in concentration of solution drunk; (*b*) variation in concentration of solution loaded into the stomach and solution drunk; (*c*) variation in the volume and concentration of gastric load and concentration of solution drunk; (*d*) variation in the delay between loading and drinking with different volumes and concentrations of gastric load and different concentrations of solutions drunk; (*e*) variation in concentration of solution drunk without involvement of any gastric factors (animals with esophageal fistulas).

The results of these experimental treatments are as follows:

1. Drinking increases as a function of concentration of solution drunk up to the isotonic point, and then it decreases (preference-aversion function).
2. Hypertonic loads elevate the drinking of water and hypotonic solutions, and depress the drinking of hypertonic solutions. Comparable water loads depress the drinking of water and hypotonic solutions, and elevate the drinking of hypertonic solutions.
3. Volumes of load as small as 0.5 cc. affect drinking as described in (2) above; but volumes as large as 10.0 cc. tend to depress drinking under all conditions except where 3 per cent NaCl is loaded and water is drunk. In this one condition, drinking is elevated dramatically.
4. Making animals wait for 1 hr. between loading and drinking yields substantially the same result as allowing them to drink immediately after loading.
5. Animals with esophageal fistulas exhibit preference-aversion curves for sodium chloride; but their ingestion of hypertonic solutions is much higher than that of control animals, pointing to the inhibitory role of hypertonic solutions in the stomach in the normal animal.

These results are interpreted to show that water drinking and the drinking of salt solutions are under the control of at least three factors: taste and other sensory mechanisms in the mouth, gastric distension, and dehydration produced by the osmotic effects of hypertonic solutions on the stomach. The ascending limb of the preference-aversion is partly a matter of response to dehydration, but, more particularly, is an increasing response to increasing

taste stimulation. The descending limb is partly due to negative stimulation of the mouth, but is largely the result of the increasing inhibition of drinking produced by increasingly hypertonic solutions in the stomach.

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Received August 17, 1953.

FOOD INTAKE OF THE RAT FOLLOWING THE INTRAGASTRIC ADMINISTRATION OF "HUNGRY" AND "SATIATED" BLOOD[1]

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It has been suggested that hunger may be hormonally governed in the sense that: (*a*) food privation is accompanied by the build-up in the blood stream of an agent capable of exciting hunger ("hunger" hormone), or (*b*) the ingestion of food releases an agent capable of inhibiting hunger ("satiation" hormone) (3, 5, 6). An earlier article by Siegel and Taub (9) has presented evidence negative to this hypothesis. It was shown that the immediately subsequent food intake of rats injected intraperitoneally with blood serum drawn from food-deprived donors was equal to that of animals similarly injected with blood serum drawn from satiated donors.

The purpose of the present study is a dual one. First, the nature of the statistical argument for nonsignificance dictates a repetition of the earlier study, employing the same general methodology. Second, the effect of administering the hypothetical blood agent via another assimilation channel seems worthy of examination. It is conceivable that the findings of the first experiment are a function of parenteral administration. In the present experiment, the intragastric route was utilized.

METHOD

One hundred and thirty-nine male albino rats of the Sherman strain, ranging in age from 82 to 114 days, were employed as *S*s. Weights ranged from 180 to 401 gm., with a mean value of 281 gm. Seventy-one animals comprised the donor group. The remainder served as recipients. Since weaning, all animals had been maintained on Purina Laboratory Chow checkers. In crushed, dry form, this is the "food" referred to throughout the experiment. The temperature of the laboratory fluctuated irregularly between the two extremes, 81° and 86°F. in the course of the three-week study. Relative humidity varied from 59 to 69 per cent.

Half the donor group contributed "hungry" blood; the other half, "satiated" blood. The former subgroup was sacrificed in the following manner: After 24 hr. of food privation (plus or minus 10 min.) with water present at all times, each animal was surgically anesthetized in a procedure standardized in preliminary observations. The rat was placed under a bell jar with an ether-soaked wad of cotton contained in an inverted screen-wire basket. There *S* remained for a 3-min. interval following the loss of all startle response to a loud tapping on the exterior surface of the jar. Parenthetically, the loss of "consciousness" in this situation is remarkably constant from animal to animal. In our study, this interval ranged from but 2 to 5 min. The rat was removed from beneath the jar, and the heart was exposed by sectioning the ribs and diaphragm on the left side. A direct heart puncture was made with a hypodermic syringe (20-gauge needle), and blood was withdrawn in the amount of 5 to 9 cc., transferred immediately to a shallow Pyrex dish, and defibrinated. The serum was then centrifuged for approximately 20 min., and the supernatant fluid was drawn off. This was added to a total serum pool that was kept stoppered and refrigerated at 5° to 7°C. for approximately 4 hr. before utilization. The latter subgroup was treated in identical fashion after ad libitum feeding (and drinking).

The recipient animals were given the experience of four days' ad libitum feeding from nonspilling food cups, and then randomly divided into two subgroups. To assure the oral intake of the serum, all animals were food- and water-deprived for 24 hr. (plus or minus 2 min.). At the end of this interval, serum (at room temperature) was offered in a drinking tube, and a 10-min. period of ingestion was permitted. Approximately one half the recipient rats were offered 3 cc. of "hungry" serum; the other half, 3 cc. of "satiated" serum. Eleven of 35 animals belonging to the former subgroup, and 9 of 33 belonging to the latter, failed to meet the intake criterion (total ingestion within the 10-min. interval) and were discarded at this stage. Following a 20-min. absorption period, a weighed food cup was placed within the cage of each of the qualifying animals, and a calibrated water bottle was attached. The food cup was reweighed to the nearest 0.1 gm., and the water bottle read to the nearest 0.5 ml. at the end of a 2-hr. intake interval (plus or minus 1 min.). Records were obtained for 24 animals in each group, with the measured intake interval falling randomly somewhere within the diurnal period, 9:30 P.M. to 12:50 A.M.

RESULTS AND DISCUSSION

Body weight is positively related to both food and water intake (7, 8). Our inability to predict whether or not a given animal would be included in the final sample, i.e., would totally drink the serum as offered, made difficult the desirable procedure of exactly matching experi-

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[1] This research was supported in part by a grant from the Research Committee of the University of Alabama.

TABLE 1

Food and Water Intake Immediately Following the Oral Administration of "Hungry" and "Satiated" Blood

	ANIMALS RECEIVING "HUNGRY" BLOOD	ANIMALS RECEIVING "SATIATED" BLOOD	t	p
Mean food intake in gm. per 100 gm. body weight	3.24 ± .66	3.19 ± .73	.250	>.50
Mean water intake in ml. per 100 gm. body weight	5.17 ± 1.09	5.51 ± 1.50	.881	>.30

mental and control recipients with respect to this variable. Our procedure resulted in a slight discrepancy in mean weight for the two groups (279 versus 294 gm.). To put all animals on a common scale, food intake was divided by body weight to yield intake per 100 gm. of body weight. Means and standard deviations of these values are presented for both recipient groups in Table 1.

Water intake, calculated in the same fashion, is also presented in Table 1. The means and standard deviations are based upon 23 cases. One animal in each group dislodged and broke the water bottle during the 2-hr. interval. A fresh bottle of water was immediately substituted, but, of course, the two water intake records were lost. For our purpose, these values are of incidental interest. Water intake was measured simply as a further control.

Table 1 indicates that the average food and water intake of the two groups is quite similar in magnitude. In both instances, the near identity of the two means suggests that a statistically significant difference is unlikely. This is confirmed by the t analyses summarized in Table 1. Our results are in agreement with the earlier study in which the serum was administered intraperitoneally. We find no difference in the immediately subsequent food intake of rats receiving "hungry" as opposed to "satiated" blood.

Within the context of a comprehensive discussion of gastrointestinal hormones, Grossman has admonished:

> A common error in the interpretation of experiments designed to test whether a humoral mechanism exists is to conclude from a negative experiment that the postulated mechanism does not exist. Actually, all that can be said from a negative experiment is that "if the postulated humoral mechanism exists it cannot be demonstrated by the methods employed" (2, p. 35).

These remarks are apposite here. Some defense of both the adequacy and validity of our experiment is suggested.

Forty-eight recipient animals constitute a reliable sample; and 3 cc. of serum seems a dosage sufficient to produce a measurable effect. Farris and Griffith (1) have summarized two studies estimating the blood volume of the rat at 4.3 cc. and 6.7 cc. per 100 gm. of body weight, with heavier animals yielding a smaller ratio. Both studies utilized the dye-disappearance method, which probably overestimates the blood volume of the animal by a considerable margin (4). Our average donor weighed 281 gm. If we adopt as a standard 5 cc. per 100 gm., we arrive at an average total blood volume of approximately 14 cc. per donor, and this is probably an overestimate. Three cubic centimeters of "hungry" whole blood or "satiated" whole blood presumably would contain about 21 per cent of the total amount of circulating excitatory or inhibitory hormone. Three cubic centimeters of serum should contain a percentage roughly double this figure if we make the logical assumption that the hormone is contained in the plasma rather than the cells. Forty per cent of the available hypothetical agent seems a conservative estimate of the amount actually ingested by our experimental animals in the present study.

We conclude that our experiment casts considerable doubt on the hormone hypothesis.

SUMMARY

Blood serum drawn from food-deprived donors was administered orally to rats following a 24-hr. fast. The immediately subsequent mean food intake, measured over a 2-hr. interval, did not differ from that of a second group administered volumetrically equal doses of blood serum drawn from surfeited donors. It was concluded that this finding casts doubt on the hormone hypothesis of hunger regulation.

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Received August 3, 1953.

THE GALVANIC SKIN RESPONSE FOLLOWING ARTIFICIAL REDUCTION OF THE BASAL RESISTANCE[1]

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The high, positive correlation between basal levels and short-term variations in skin resistance (1, 3) seriously complicates the task of measuring the galvanic skin response (GSR). Owing to the wide variation in basal levels (from a few thousand ohms to more than 150,000) and the practical limitations imposed on the width of recording tapes, provisions must be made for rapid and accurate changes both in the value of the base line and in the attenuation of the amplifying system. As a result, not only the apparatus employed but the recording procedure and the subsequent interpretation of records become unduly complex. Another consequence of the correlation between basal level and magnitude of response is the difficulty involved in the analysis of individual differences in reactivity—response magnitudes must be mathematically transformed to eliminate the influence of basal level (1, 2, 3).

It may be seen, therefore, that experimental work with the GSR would be considerably simplified by the elimination of individual differences in basal resistance. One way to accomplish this purpose would be to reduce artificially the basal resistances of all *S*s to the same low level—e.g., by rubbing the skin with electrode paste. Although it might be supposed that such a procedure would result only in the removal of an inert resistance from the circuit, there is evidence that the GSR is affected by changes in basal level resulting from any cause (4). The effects of artificially induced changes in level have not, however, been systematically studied, and it is conceivable that the procedure might introduce serious artifacts. The experiment here reported, which is primarily a methodological one, was intended to investigate this possibility. It was designed to explore the effect of artificial reduction in the basal level of resistance on the magnitude of the GSR.

METHOD

Subjects

The *S*s employed for the experiment were 192 students of both sexes at the University of Texas who were assigned at random to three experimental groups. The number of *S*s in each group was 64.

Apparatus

To make simultaneous measurements of the GSR at each of *S*'s hands, two identical apparatuses were employed. Resistance was measured between the palmar and dorsal surfaces of each hand. Sponge-rubber electrodes, saturated with a saline solution, filled plastic cups (1.5 in. in diameter) which were strapped to the surfaces of the hand. The rubber disks made pressure contact with zinc plates set into the backs of the plastic cups, and to these plates leads were soldered which ran to a balancing and scaling device, a Brush d.c. amplifier (model BL 932), and one channel of a Brush recorder (model BL 202).

The circuit diagram of the balancing and scaling device is shown in Figure 1. A constant current through *S*'s hand was supplied by a 90-v. battery in series with *S*, a calibrated 100,000-ohm potentiometer (R_3), and other high resistances. The voltage across *S* and the potentiometer was proportional to their combined resistance at any given time. This voltage was opposed by another so adjusted that the net voltage was zero when the combined resistance of *S* and the potentiometer was 100,000 ohms. A three-position voltage divider yielded 25 per cent, 50 per cent, or 100 per cent of the voltage across *S* and the potentiometer. The output of this attenuator was led to the d.c. amplifier, which was operated at either of two levels of gain. The apparatus could thus be calibrated to read either 50, 100, 200, or 400 ohms for each 1-mm. deflection of the recording pen, depending on the setting of the voltage divider and the gain of the amplifier. The entire system was linear over the range of resistances measured in the experiment. When the two apparatuses were employed simultaneously to measure resistances at two hands, coupling effects appeared because the two amplifiers shared a common ground. A large capacitance from each amplifier to ground served to restore independence.

Procedure

The experiments were conducted in a dimly illuminated, electrically shielded, soundproof room. The *S*

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[1] This research was conducted under terms of contract AF 33(038)13387 between the United States Air Force and the University of Texas in coordination with the Department of Clinical Psychology, USAF School of Aviation Medicine, Randolph Field, Texas.

was seated in a comfortable, leather-upholstered chair, with his arms resting on the broad armrests, and instructed only that "certain physiological measurements" were to be made. He was asked to sit quietly in the chair and to save any questions that he might have until the termination of the session. The GSR electrodes were attached, one pair to each hand, the circuit was balanced, and a few moments were allowed to elapse during which *S* had the opportunity to adjust to the recording situation. Then two stimuli were automatically presented in sequence. Each stimulus was 3 sec. in duration, and the interval between them was 30 sec. The first stimulus (S_1) was a flash of light from a 100-w. tungsten lamp in a common gooseneck reflector directed at *S*. The second stimulus (S_2) was a 1000-cycle tone of moderate intensity produced by an audio-oscillator connected directly to a speaker behind *S*'s chair. Presentations of the stimuli were recorded simultaneously on one channel of each of the two Brush recorders (the other channel of each recorder being activated by one of the GSR circuits). Data for each *S* were taken by two *E*s, one monitoring each of the recording systems, and independent analyses of the two recording tapes subsequently were made.

Both hands (H_1 and H_2) of each *S* in group I (the *treated* group) were rubbed with electrode paste prior to the attachment of the electrodes.[2] If this treatment did not reduce the resistance of either hand to a level below 10,000 ohms, the electrodes were removed and the treatment repeated. Thus, the basal resistance of each hand of each *S* was less than 10,000 ohms. Both hands of each *S* in group II were *untreated*—the electrodes were attached without rubbing electrode paste into the skin. For group III, one hand (H_1) was treated (in the same manner as both hands of group I), and the other hand (H_2) was untreated. To randomize any lateral differences that might exist, each group was divided by lot into two equal parts. For half of each group the right hand served as H_1 and the left hand as H_2, while for the other half of each group the left hand served as H_1 and the right hand as H_2. Only in the case of group III was the actual experimental procedure determined by these designations (i.e., H_1 was treated and H_2 untreated), but they were significant for the other two groups in that the data were analyzed in terms of these designations rather than anatomically.

RESULTS

The first step in the analysis of the results was to find an index of the GSR suitable for comparing treated and untreated hands. For this purpose change in resistance (ΔR) produced by each stimulus in each hand of each *S* in all three groups (a total of 768 responses, half from treated and half from untreated hands) was plotted against basal resistance (R). Since the relation proved to be satisfactorily linear, it was possible to eliminate the influence of basal level by dividing ΔR by R. The distribution of $\Delta R/R$ was found to be positively skewed, but a square-root transformation resulted in a distribution which did not depart significantly from normality. Consequently, the unit employed in the analysis was $(\Delta R/R)^{\frac{1}{2}}$. Table 1 shows the mean responses of treated and untreated hands to each of the stimuli. The derived response distributions were almost identical despite great dissimilarity in basal resistance.

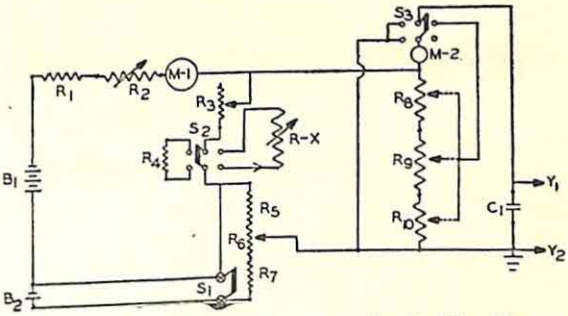

FIG. 1. Balancing and scaling circuit (B_1, 90 v.; B_4, 7½ v.; C, 1.0 microfarad; M_1, microammeter; M_2, microammeter; R_1, 1,500,000 ohms; R_2, 200,000 ohms; R_3, 100,000 ohms; R_4, 50,000 ohms; R_5, 6,000 ohms; R_6, 10,000 ohms; R_7, 12,000 ohms; R_8, 540,000 ohms; R_9, 270,000 ohms; R_{10}, 266,000 ohms; R–X, S's resistance; S_1, DPST; S_2, DPDT; S_3, DPDT; Y_1–Y_2, output to amplifier).

TABLE 1

Mean Basal Resistance and Response to Each Stimulus in Treated and Untreated Hands

HAND	S_1		S_2	
	R	$(\Delta R/R)^{\frac{1}{2}}$	R	$(\Delta R/R)^{\frac{1}{2}}$
Treated	5456	.182	5312	.211
Untreated	34182	.178	37469	.215

Four separate measures were available for analysis in each group: (*a*) the response of H_1 to S_1; (*b*) the response of H_1 to S_2; (*c*) the response of H_2 to S_1; and (*d*) the response of H_2 to S_2. Product-moment correlation coefficients were computed among these four variables for each of the three experimental groups. These intercorrelations are presented in Table 2.

Each of the correlations is, of course, affected by statistical unreliability owing to errors of measurement. Other factors which may attenuate the various coefficients suggest themselves upon consideration of the conditions

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[2] The paste used was manufactured by the Burdick Corporation of Milton, Wisconsin.

TABLE 2

Intercorrelations for the Three Experimental Groups*

	GROUP I	GROUP II	GROUP III		
			r obtained	*r corrected*	Common variance (%)
r_{ac}	.74	.61	.61	.91	83
r_{bd}	.67	.62	.28	.43	18
r_{ab}	.75	.74	.77		
r_{cd}	.76	.73	.72		
r_{ad}	.54	.35	.33	.76	58
r_{bc}	.48	.48	.51	1.06	100

* (*a*) H_1S_1, (*b*) H_1S_2, (*c*) H_2S_1, (*d*) H_2S_2.

for each group. The correlation between responses of H_1 and H_2 to a given stimulus (r_{ac} for S_1 and r_{bd} for S_2) is lowered by any differences between the two hands. In group III this lateral correlation is attenuated further by any differences due to treatment. The correlation between responses of the same hand to the two different stimuli (r_{ab} for H_1 and r_{cd} for H_2) is affected both by changes in the individual through time and by differences between the two stimuli (light and tone). The remaining two correlations for groups I and II (r_{ad} and r_{bc}) are still further attenuated since they reflect lateral differences as well as differences due to time and stimulus. For group III, these coefficients reflect all four sources of variability—laterality, time, stimulus, and treatment.

Examining first the coefficients for groups I and II (Table 2), we find that the two arrays are quite similar. The temporal correlations (r_{ab} and r_{cd}) are slightly higher than the lateral correlations (r_{ac} and r_{bd}); and, as expected, the smallest coefficients are those that are affected both by temporal and by lateral variability (r_{ad} and r_{bc}).

The array for group III is similar to the other two arrays with one marked exception—the lateral coefficient for S_2 (r_{bd}). The correlations of primary interest are those in group III which reflect differences in the two methods of treatment (r_{ac}, r_{bd}, r_{ad}, r_{bc}). In every case, however, treatment is confounded with lateral variability, either alone or in combination with variability due to time and stimulus. Without the results for groups I and II it would be impossible to estimate the extent to which differences in treatment lowered these four correlations in group III. Since identical stimulating conditions and comparable *S*s were used in each of the groups, however, it should be possible to estimate from the coefficients for groups I and II what the correlations for group III would have been if all sources of variability except differences in treatment could have been eliminated.

For example, consider the correlation between the responses of H_1 and H_2 to S_1 (r_{ac}). In group III, the proportion of variance in *a* which is attributable to variation in *c* is only .37 (r_{ac} = .61). Part of the variance in *a* which is not accounted for by r_{ac} may be due to differences in the treatment of the two hands; part of the residual variance in *a* may be due to lateral variability; and part of it may be attributed to random errors of measurement. For the same correlation in groups I and II, the residual variance in *a* is accounted for by only two of these components, lateral variability and random error. On the assumption that the lateral effect and the random errors of measurement are approximately equal for the three groups, the critical difference between group III and the other two groups lies in the effect of treatment, the factor of primary interest in the present study. Correcting the obtained r_{ac} of group III for attenuation by Spearman's formula for estimating the correlation between true scores in each of two measures, we get a coefficient of .91. We estimate, therefore, that 83 per cent of the variance in *a* can be attributed to variation in *c* after the influence of laterality and error of measurement has been eliminated.

The same kind of reasoning can be applied to the other correlations for group III which involve differences in treatment—r_{bd}, r_{ad}, and r_{bc}. The obtained and corrected coefficients are presented in Table 2. From this table it may be seen that the percentage of variance in the response of one hand which can be attributed to variation in the response of the other hand (after all sources of variance except treatment have been removed) ranges from 18 for the second lateral correlation (r_{bd}) to 100 for one of the lateral-temporal correlations (r_{bc}). The wide variation in the estimated degree of communality between the two treatments suggests that under some conditions they yield markedly similar results, while under others they may differ appreciably in the extent to which they reflect the same underlying response mechanism.

To help clarify this situation a factor analysis was made of the correlation matrix for each group by Thurstone's centroid method (5). Because each matrix was very small, each analysis was repeated several times until the obtained communalities agreed closely with the estimated communalities that had been entered in the diagonal cells of the matrix at the start of the analysis. The question was asked: How much of the communality in each correlation matrix can be accounted for by a single general factor? To answer this question it was necessary to place the first reference axis of each factor matrix so as to maximize the sum of squares of its factor loadings. Following Thurstone (5, pp. 473–480), a transformation matrix was found for each centroid-factor matrix which, when premultiplied by the centroid-factor matrix, gave a principal-axes solution. Such a factor matrix for the principal axes is a unique solution for any given correlation matrix and has the important property that the r-factor residuals are at a minimum.

All three matrices (Tables 3, 4, and 5) reveal high loadings on the first factor, which substantiates the hypothesis that most of the variance in the test variables can be attributed to the same underlying response mechanism. The average variance for each factor is given in the bottom row of each table. Group I, the treated group, shows the greatest consistency of response from one hand to the other and from one stimulus to the next, as indicated by consistently high loadings on factor A, the general factor. The percentage of the total variance attributable to this general factor is highest in group I, somewhat less in group II, and lowest in group III.

For groups I and II, two other factors can be extracted. Factor B seems to reflect lateral differences, and factor C is derived from differences due to time and stimulus. The average variance of each of these factors is relatively small and quite similar for the two groups. The three factors in combination account for 92 per cent of the variance in group I and 89 per cent of the variance in group II. Reliability of measurement thus appears to be quite high both in the treated and untreated hands—slightly higher, if anything, in the treated hands. The marked similarity of the factor patterns for the two groups suggests that treatment (reduction of basal resistance by the method here employed) does not adversely affect either the reliability or the validity of measurement.

The results of the factor analysis for group III (Table 5) differ to some extent from the results for the other two groups. In the data of group III the general and lateral factors (A and B) are in evidence, but the effect of differences in time and stimulus (represented in the other groups by factor C) is not reliably measured. Communality is considerably lower in group III than in the other groups,

TABLE 3

Factor Loadings for Group I, Principal-Axes Solution

VARIABLE	FACTOR			h^2
	A	B	C	
H_1S_1	.87	−.26	−.32	.93
H_1S_2	.82	−.42	.23	.90
H_2S_1	.86	.39	−.23	.94
H_2S_2	.85	.27	.35	.92
Factor variance (%)	72	12	8	92

TABLE 4

Factor Loadings for Group II, Principal-Axes Solution

VARIABLE	FACTOR			h^2
	A	B	C	
H_1S_1	.80	−.44	−.29	.92
H_1S_2	.83	−.34	.29	.89
H_2S_1	.84	.36	−.29	.92
H_2S_2	.78	.39	.30	.85
Factor variance (%)	66	15	8	89

TABLE 5

Factor Loadings for Group III, Principal-Axes Solution

VARIABLE	FACTOR		h^2
	A	B	
H_1S_1	.83	.39	.83
H_1S_2	.75	.40	.72
H_2S_1	.89	−.38	.94
H_2S_2	.61	−.46	.59
Factor variance (%)	61	16	77

with only 77 per cent of the variance being accounted for by common factors. Of the four measures for group III, the response of H_2 (the untreated hand) to S_2 shows the smallest communality and the smallest loading on the general factor. The deviant character of this measure is also apparent in the array of coefficients for group III, presented in Table 2. Of the four corrected lateral coefficients, the two which involve H_2S_2 (r_{bd} and r_{ad}) are relatively low, while the others are quite high. It seems likely, therefore, that the deviant results for group III may be attributed to experimental error in the measurement of H_2S_2. The source of this error has not been definitely determined.

In general, then, the results of this experiment give no reason to believe that the reduction of basal resistance by rubbing the skin with electrode paste distorts the GSR in any significant fashion. The pattern of response in the treated hands of group I corresponded closely to the pattern of response in the untreated hands of group II. Only in group III was there a lack of complete correspondence between the two conditions, and this discrepancy could be traced to instability in the untreated hand. It may be concluded, therefore, that the advantages derived from the artificial reduction of basal resistance by the method here employed are not gained at the expense of reliability or validity of measurement.

SUMMARY

The experiment reported was designed to study the effect of artificial reduction of the basal resistance (by rubbing the skin with electrode paste) on the galvanic skin response. For each of 192 *S*s simultaneous measures of the GSR in both hands were made. In one group both hands were treated with electrode paste; in a second group both hands were untreated; and in a third group one hand was treated and the other untreated. The reliability of measurement was in general high under each of the two conditions, and the results suggested that the GSR was not significantly distorted by artificial reduction in the basal resistance.

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Received July 17, 1953.

RATE OF BAR PRESSING AS A FUNCTION OF QUALITY AND QUANTITY OF FOOD REWARD[1]

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Quality and quantity of reinforcement have frequently been suggested as important variables influencing the performance of learned and unlearned responses. A number of studies have supported this suggestion (3, 4, 5, 6, 7, 8, 12, 13, 14, 15, 17, 18). Quality of food reward has been used to designate different kinds of natural foods among which there is an implied difference in preference. Most of the experiments on quality have varied concurrently the taste, odor, texture, and nutritive variables, which, according to Skinner (16), should be treated separately. Quantity of reward has usually referred to differences in weight, volume, concentration, number of pieces of food, and time of eating. While these variables are often related, their effects may not be equivalent, as pointed out by Guttman (8).

The complexity of the concepts of quality and quantity necessitates a systematic study of their more specific aspects. The present experiment deals with amount; with one aspect of quality, taste; and with their possible interaction. Variations in taste were produced by adding citric acid or saccharin to a basic food mixture. This technique permitted control of color, odor, texture, and nutritive value. Variations in weight were associated with different volumes of the reinforcing material; the variable of amount, therefore, comprises both weight and volume. The three tastes were combined with three amounts in a factorial design, resulting in nine combinations of taste and amount. The design allows for an evaluation of possible interaction between taste and amount.

These variables were studied in relation to performance. The measure used was the rate of a periodically reinforced bar-pressing response in the Skinner-box situation.

METHOD

Apparatus

The apparatus consisted of three identically constructed Skinner boxes. The *S*'s compartment was a 12-in. cubical aluminum box enclosed in a sound-insulating shell. The interior surface of the box was uniformly burnished and was illuminated by a 4-w. fluorescent lamp behind an opal glass window in the lid. The compartment was ventilated by a steady flow of air produced by an electric blower. The blower also provided a masking sound for extraneous noises. A 5-in.-diameter circular window in the lid permitted observation of *S* during the experiment.

In the center of one wall of the box, a ¼-in. steel rod protruded 1¼ in. horizontally into the cubicle. This bar was 3½ in. above the floor. Directly below the bar, in the floor of the box, was a small hole through which the food dipper was presented. The size of the hole was adjusted to the size of the dipper being used. The magazine was automatically operated by depressing the bar, and could also be controlled by *E*.

The capacities of the dipper cups were 3, 12, and 50 mg. The amounts used were intentionally small in order to obtain bar-pressing rates close to the threshold of response. In this report, the three cup sizes used are referred to as small, medium, and large.

The 1-min. periodic reinforcement schedule employed in the experimental sessions was obtained by use of a synchronous clock motor and a relay circuit.

Reinforcing Substances

The basic reinforcing substance used was a homogeneous semiliquid mixture of flour, milk, and water. This is a modification of the standard adequate diet for rats recommended by the Nutrition Laboratory, Teachers College, Columbia University (2).[2] The different reward substances were made as follows: Basic mixture: 370 gm. basic food diluted with 30 cc. water; citric mixture: 370 gm. basic food diluted with 30 cc. of a 20 per cent citric acid solution by weight; saccharin mixture: 370 gm. basic food diluted with 30 cc. water containing 9 gr. of soluble saccharin. This concentration of saccharin (22.5 gr. per liter) was reported by Beebe-Center *et al.* (1) to be optimally preferred over water by rats. The amount of citric acid used was found by trial and error to be barely acceptable to rats in preliminary preference tests. In these tests, with the three foods presented simultaneously for choice, food containing citric acid in the concentration used was rarely eaten, while, when citric mixture was presented alone, the amounts eaten were similar to the amounts of basic and saccharin mixtures eaten at other times.

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[1] This paper is based on a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School of Duke University, 1953.

[2] The basic substance was prepared according to the following recipe: Combine 2 cups cold water, 100 gm. enriched white flour, and ½ cup evaporated milk. Add 2 cups hot water and heat to boiling. Add 1⅓ cups cold water. A fresh batch of food was made each day.

Subjects and Procedure

The *S*s were 81 experimentally naive male albino rats obtained from Albino Farms, Red Bank, New Jersey. They were between 90 and 110 days old at the beginning of the experiment. After arrival from the dealer, the rats were kept in individual cages for ten days, with free access to food and water. On the eleventh day the animals were started on a 23½-hr. feeding schedule, which lasted seven days. A mash made from ground Purina Kibbled Meal mixed with an equal volume of water was placed in the cage for ½ hr. daily. Water was available at all times.

On the eighth day of scheduled feeding, *S*s were put into the Skinner box 45 min. before their customary feeding time and trained to eat food from the magazine. The bar was absent, and *E* presented food by operating a switch. Magazine training was carried out for six daily ½-hr. experimental periods. On the first three days, *S* received six to eight dippers of food in each period; during the last three days the rate of presentation was increased. Every *S* received 75 dippers of food during the six-day period. The basic mixture (without saccharin or citric acid) and the medium dipper (12 mg.) were used.

At the end of each experimental session, *S*s were returned to their home cages, and approximately 15 min. later they received their regular ½-hr. feeding.

On the day following the last session of magazine training, *S*s were placed in the Skinner box with the bar present for the first time, and were put on a continuous reinforcement schedule. The basic mixture and the medium dipper were used. This training extended over seven ½-hr. sessions. Each *S* was given 150 reinforcements spaced over a period of six days. On the seventh day each *S* received 50 reinforcements, making a total of 200 reinforcements for the seven days. If any *S* received 150 reinforcements before the sixth day, it was fed at the customary time but not put into the box again until the seventh day, when 50 additional reinforcements were given. The *S*s were fed wet mash for ½ hr. after each session as before.

On the day following the last continuous reinforcement day, *S*s were assigned at random to nine experimental groups, nine animals in each group. They were then given five successive daily sessions of periodic reinforcement (PR) for bar pressing. During all five PR sessions each group received one of the nine possible combinations of dipper size and food: (*a*) small-saccharin, (*b*) medium-saccharin, (*c*) large-saccharin, (*d*) small-basic, (*e*) medium-basic, (*f*) large-basic, (*g*) small-citric, (*h*) medium-citric, and (*i*) large-citric.

A 1-min. PR schedule was used for all groups, and all experimental sessions were ½ hr. long; there were 30 reinforcements per session. Following each session *S* was fed in the home cage, as before.

Possible differences among boxes were controlled by using each box an equal number of times under each of the experimental conditions; that is, each box was used for three rats in each of the nine experimental groups.

Twenty-four hours after the last session on PR, *S*s were put into the apparatus with the bar in place, but disconnected from the magazine. The *S* remained in the box for ½ hr. and then was fed as before. This extinction procedure was carried out on two successive days.

Following extinction, 27 *S*s were given preference tests in their home cages. Each of the three foods was placed in an aluminum cup with a capacity of 60 gm. Cups were inserted in aluminum trays to hold them securely. The tray with the food-filled cups was put in the back of the home cage and left there for ½ hr. After that time all trays were taken out of the cages and the remaining food was weighed. The regular feeding was omitted, and the preference test was repeated 23½ hr. later.

RESULTS

The mean rate of responding, in responses per minute, for the three tastes and the three amounts on each of the five days of PR is presented in Figure 1. Analysis of variance on log mean PR rates for days 1 and 5 both show the main effects of taste and amount to be significant at better than the .005 level. Thus, the rate of performance of a bar-pressing response is an increasing function of the amount of reinforcement for the values 3, 12, and 50 mg., and is also related to the taste of the reinforcing substances. A nearly significant interaction at the .05 level is present on day 1 ($F = 2.40$; $df = 4, 72$). On day 5 the test for interaction results in a clearly insignificant value ($F = 0.31$; $df = 4, 72$).

The mean responses per minute for all groups on days 1 and 5 are shown in Table 1. There is essentially no change in the response rate for

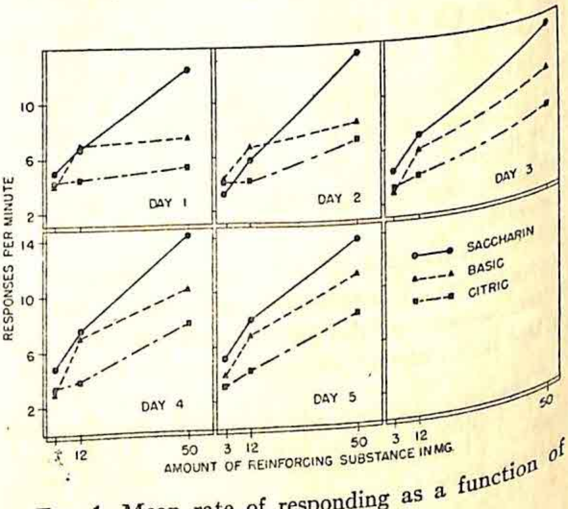

FIG. 1. Mean rate of responding as a function of amount of reinforcing substance

TABLE 1

Mean Responses per Minute for Days 1 and 5

AMOUNT	CITRIC		BASIC		SACCHARIN	
	Day 1	Day 5	Day 1	Day 5	Day 1	Day 5
Small	4.2	3.0	4.1	3.9	5.0	5.0
Medium	4.5	4.2	6.8	6.9	6.7	8.0
Large	5.3	8.2	7.5	11.1	12.5	13.8

TABLE 2

Significance of Differences Obtained by *t* Tests between Log Mean PR Rates of Responding on Days 1 and 5 for Taste and Amount

(Asterisks denote differences at the .05 level or less.)

Taste

AMOUNTS COMPARED	DAY 1			DAY 5		
	Saccharin	Basic	Citric	Saccharin	Basic	Citric
Small and medium		*		*	*	
Small and large	*	*		*	*	*
Medium and large	*			*	*	*

Amount

TASTES COMPARED	DAY 1			DAY 5		
	Large	Medium	Small	Large	Medium	Small
Saccharin and basic	*					
Saccharin and citric	*	*		*	*	*
Basic and citric		*			*	

the groups reinforced with the small and medium amounts, except for the medium-saccharin, which increases, and for the small-citric, which decreases. There is, however, an increase in the rate of responding to the large amount for all tastes.

Table 2 gives the significant differences between the various tastes and amounts for days 1 and 5. It can be seen that with the particular qualities and quantities used, differences in amount are a more potent determinant of response rate than are differences in taste. Although five of the taste differences did not approach statistical significance, it is evident from an inspection of Figure 2 that the influence of the two variables, taste and amount, is reflected in the differences in the slopes of the nine curves. Mean response rates are in descending sequence from large to small with respect to amount, and from saccharin to citric with respect to taste, except for small-citric with respect to taste, except for small-saccharin, which is greater than medium-citric. These mean PR rates are practically linear, indicating a uniform level of performance for each group. Within any experimental session, there is, however, a slight decline in the rate of responding in successive 5-min. periods; large-saccharin is the only exception to this trend.

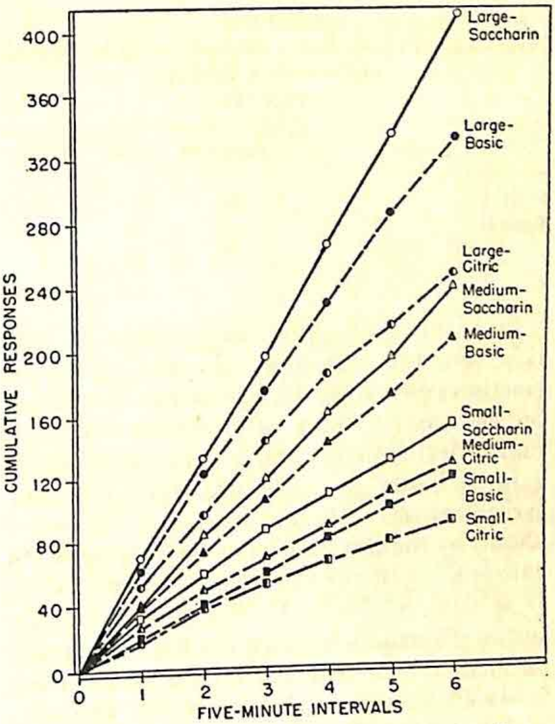

FIG. 2. Mean cumulative PR curves for day 5

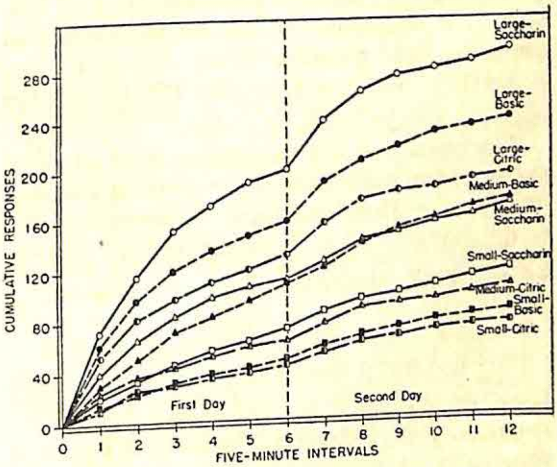

FIG. 3. Mean cumulative curves for two ½-hr. periods of extinction after PR

TABLE 3

Percentage of Foods Eaten during Two ½-hr. Periods of Preference Testing

($N = 27$)

TEST	SACCHARIN	BASIC	CITRIC
First	66	29	5
Second	89	10	1
Total (2 tests)	79	18	3

In Figure 3 are presented the mean cumulative response curves for the two ½-hr. extinction periods. Again, an analysis of variance on log mean number of responses shows the main effects of taste and amount to be significant at better than the .005 level. The similarity between PR and extinction is further shown by the correlation between log mean PR rate and log number of responses in extinction ($r = 0.90$; $SE_r = 0.11$). The trend of the size of the differences between the first and second extinction periods is the reverse of the trend in the PR rates from day 1 to day 5. The order and size of the differences in the first extinction period closely resemble those on day 5 of PR, while the differences in the second extinction period closely resemble those on day 1. This is further evidence that the PR trend over successive days is not an artifact.

The results of the preference tests on 27 of the experimental animals are given in Table 3. They show that saccharin is preferred over basic, and that basic is preferred over citric in a free-choice situation.

DISCUSSION

The results of the present experiment show that the rate of performance of a learned response in a free-responding situation is a function of the quantity and quality of reinforcement. This finding is in general agreement with the results of previous experiments that used different situations, different response measures, and different dimensions for the measurement of quantity (3, 6, 7, 8, 12, 17). The relatively consistent results of the present study may in part be attributed to the large number of responses recorded, the explicit specification of the stimulus dimension, and the use of periodic reinforcement.

The fact that there was no interaction between quality and quantity reveals the additive nature of their reinforcing effects. This confirms the results of Fay, Miller, and Harlow (5), who found that quality and quantity are independent determinants of choice frequency.

The present results agree with studies reported by Skinner (16) and Jenkins (11), showing that the PR situation is exceptionally sensitive to the variables influencing performance. This is confirmed by the fact that, within the limits of individual variability, there appears to be, in at least the present experimental situation, a linear relation between log rate of responding and log number of responses in extinction. On the usual assumption that number of responses in extinction is a measure of habit strength, it would seem likely that the use of periodic reinforcement as a direct measure of habit strength could be generalized to other learning and performance situations.

The results further suggest a method for the treatment of two types of problems. The first would be the problem of scaling "kinds" or "qualities" of reinforcement. The PR method seems to be very sensitive to small variations in the properties of the reinforcing agent. This is particularly interesting, both theoretically and experimentally, because of the apparent association between the preference order and the rate of responding. The second problem that might be treated by this method would be that of determining sensory thresholds to chemical differences in the reinforcing agent.

One question that may be raised about the definition of quantity used in the present experiment is whether weight or volume is the important aspect of the reinforcement. Variations in weight were associated with variations in volume, leading to possible differences in the ingestive effect. This may be contrasted with the technique used by Guttman (8), who varied concentration and held volume constant. Both techniques show that performance varies as a function of quantity of reinforcement, but this statement cannot be quantitatively specified.

While "quality" of reinforcement has been stated by Hull (10), Skinner (16), Young (18), Harlow (9), and others to be an important property of the reinforcing agent, the specification of the quality variable has remained vague. Typically, it has referred to the fact that within a given class of reinforcements, such as food, there are differences in kind, and it has been asserted that the effectiveness of the reinforcement is associated with the *kind*. No simple rule has been devised for scaling quality in terms of physical, chemical, or nutritive (or other biological) dimensions, although some attempts have been made to scale it in terms of preference. Thus, quality and quantity represent, at the moment, fundamentally different sorts of variables. In the present study the very limited question has been asked whether or not the chemical modification of a food by substances known to differ in taste (for humans) would alter the effectiveness of its reinforcing properties, when the nutritive value, texture, appearance, etc. of the food were held constant. The results indicate that such chemical modification does alter the reinforcing effect. This suggests that the receptor processes involved in the discrimination of the modified substances play an important role in the process of reinforcement, and also points to an available physical dimension along which the quality variable might be analyzed.

SUMMARY AND CONCLUSIONS

Eighty-one rats were trained in a modified Skinner box, with three reinforcing substances differing only in taste and amount. The basic substance was a semiliquid mixture of milk, flour, and water. Two other mixtures were made by adding a saccharin or citric acid solution to the basic mixture.

Preference tests were given to 27 rats, using the foods-together technique.

The analyses of variance on rates of responding during periodic reinforcement for days 1 and 5 both showed the main effects of taste and amount to be significant at better than the .005 level of confidence. There was no indication of a significant interaction. A high positive correlation of .90 was found between log mean PR rates and responses during extinction. Results of the preference tests showed that the saccharin-flavored food was highly preferred over basic and citric.

Within the limits of the present experiment, the following conclusions may be drawn:

1. The rate of responding during periodic reinforcement is a function of both the taste and the amount of the food reward.
2. The differences in rate of responding for taste are associated with food preference.
3. A high positive correlation exists between PR rate and number of responses during extinction.

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Received September 19, 1953.

THE SECONDARY REINFORCING VALUE OF FOOD FOR THIRSTY ANIMALS[1]

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In a review of latent learning Thistlethwaite asked the following question: "Does the irrelevant incentive itself serve as a secondary reinforcing agent?" (14, p. 109). Since food-satiated (15) or thirsty (2, 13, 16) rats did not manifest a preference for a food alley over a nonfood alley in the latent period, he concluded that the answer was negative. Contrary evidence by MacCorquodale and Meehl (6) was discounted on the grounds of alleged inequalities in position preference and an inadequate satiation technique.

Without attempting an exhaustive survey of the literature, several studies relevant to Thistlethwaite's conclusion should be mentioned. Myers (8) found that satiated rats motivated by a social drive selected a food alley far more frequently than a nonfood side. When the locus of the food was shifted, they reversed their preference to conform to the new position of the irrelevant incentive. Myers' data, however, seem vulnerable to the criticism that the animals were not completely satiated, since some consummatory activity took place. More recently Johnson (5) reported that thirsty rats during the latent sessions displayed a shift toward more food-side turns, and the less thirsty rats showed greater change in this direction. No indication of the statistical significance of these data was provided. Finally, Seward and Levy (10) demonstrated that satiated rats will select a goal box in which reward was secured earlier over an end box where it was not found.

In light of this later evidence we feel, with others (7, 11), that it is essential to reconsider the above question. Our interest is not whether or not secondary reinforcement provides a feasible explanation for certain types of latent learning, but rather an inquiry into the necessary and sufficient conditions for a cue to function as a learned reward. More precisely, the question is this: Does the sight of food have secondary reinforcing properties for thirsty, food-satiated *S*s?

An examination of the studies reviewed by Thistlethwaite suggested several possible confounding factors in T-maze settings that might obscure the effects of secondary reinforcement. These were: (*a*) alternation behavior, especially when the trials were massed, (*b*) place and turn biases, which constitute a formidable problem to control, and (*c*) "emotionality" induced by the forcing of choices. Therefore, a simple runway and spaced trials are employed in an effort to reduce these sources of confounding variation. It is also hoped that running-time measurements are more sensitive indices of reaction tendency than the direction of choice. The experimental question is: Will thirsty, food-satiated rats run faster to an end box containing food than similarly motivated *S*s running to an empty end box?

METHOD

Apparatus

The apparatus was a 5-ft. alley runway constructed of 1-in. by 6-in. pine boards. The first 9 in. constituted the starting box and were painted flat white. The runway and the 14-in. by 12-in. by 7-in. goal box were painted dull black. The apparatus was covered by hardware cloth and illuminated from 6 ft. above by two 90-w. fluorescent lights.

Raising the starting-box guillotine door activated a standard timer. The clock was stopped by *S*'s weight on a hinged floor panel located at the entrance to the goal box. Another guillotine door on the goal box prevented exits from the chamber and retracing on the runway.

Pretraining Procedure

During the first five days *S*s were tamed and placed on an 8-hr. thirst cycle. On the sixth day groups of five or six *S*s explored the empty runway for 15 min. On day 7 and 8 each *S* received a single runway trial, and running times were recorded. One half hour after the last daily trial the water bottles were inserted in the home cages, where they remained until 8 hr. before the next day's runs. Throughout the experiment the home cages were well stocked with Purina Layena pellets. As an added precaution against incomplete satiation, dishes of pellets were placed in the individual handling cages in the experimental room.

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[1] This research was supported by the Faculty Research Committee, University of Kansas.

On the basis of the running times for the two individual trials, two matched groups of nine *S*s each were selected. The pairing resulted in a control group with median running times of 5.82 and 6.05 sec., and an experimental group with medians of 7.90 and 7.68 sec. The range of scores in each group was virtually identical.

Test Procedure

During the following 20-day test period *S*s were given one trial per day. The experimental group found the floor of the goal box covered with food pellets, while the control *S*s found it empty. After traversing the runway, *S*s were confined in the goal box for 20 sec. before being returned to their individual handling cages. Whenever the running time reached 300 sec., *S* was taken from the runway and placed in the goal box for the usual detention period. In the test phase *S*s were deprived of water for 8 hr. and satiated for food by the ad libitum feeding schedule.

Subjects

The *S*s were 23 experimentally naive male Sprague-Dawley albino rats 70 to 77 days old. They were purchased from the Sunset Hills Farm of Lawrence, Kansas. Five *S*s were discarded in the matching to leave two groups of nine *S*s each.

RESULTS

The basic datum, running time, was defined as the time between elevation of the starting-box door and *S*'s entry into the goal box. Figure 1 shows the median running times for the control and experimental groups during the two matching trials and the four successive five-trial test intervals. The significance of the difference between the means of the first five and the last five test trials are assessed by Wilcoxon's *T* test for paired replicates (18) in Table 1. The control *S*s ran significantly more slowly on the final test trials, and the experimental *S*s ran equally well in both test periods.

In Table 2 the differences between the experimental and control groups at successive quarters of the test are analyzed by Wilcoxon's test for paired replicates. Because one experimental *S*, on trial 13, put a pellet in its mouth, gnawed twice, and then dropped it, these differences are based on only eight pairs.[2] It is apparent that after the first five trials the control group is performing more sluggishly, and the differences increase in significance as the test trials progress.

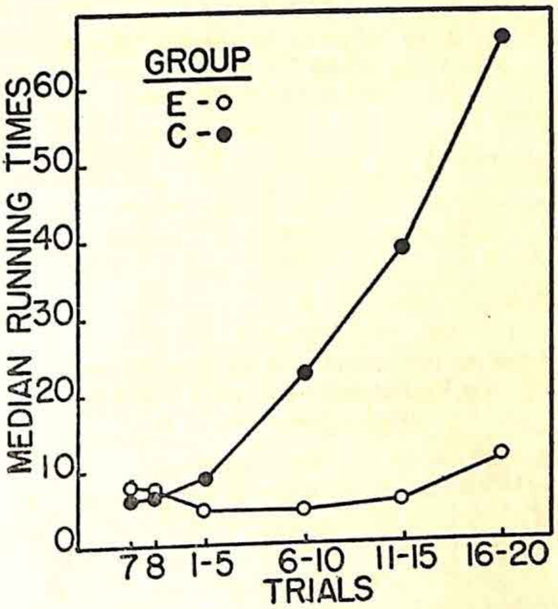

FIG. 1. Median running times in seconds during the 2 matching trials and the 20 test trials for the control and experimental groups

A further contrast between the two conditions can be made on the individual trials. If the group medians were determined by chance, we should anticipate that the experimental group's medians would be below the control group's on half the test trials, and vice versa (3). Instead, the experimental group's medians are below the control group's on trials 2 to 20. The probability of this outcome by the binomial expansion is far less than .001.

The variabilities in running time were also affected by the presence or absence of the irrelevant incentive. These differences were evaluated by the *t* test for variances based on related scores (17, p. 190). The usual *F* ratio is inapplicable in this instance because the variances are not independent. From Table 3 we may conclude that control *S*s were significantly more variable on the final test trials than they were initially, while the experimental group did not change. There was no difference between the variances of the two groups on the first five trials, but the control *S*s were decidedly more variable at the termination of training.

Finally, certain qualitative aspects of behavior should be mentioned. The *S*s dis-

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[2] In all other comparisons the exclusion of this pair of *S*s did not affect the level of statistical significance.

TABLE 1

T Tests of the Difference in Running Time on the First Five and Last Five Test Trials for the Experimental and Control Groups

MEASURE	GROUP	
	E	C
T	10	1
p	$> .05$	$< .01$

TABLE 2

T Tests of the Differences in Running Time between the Experimental and Control Groups at Successive Quarters of the Test

MEASURE	TRIALS			
	1–5	6–10	11–15	16–20
T	13	4	3	1
p	$> .05$	$.05$	$< .05$	$< .02$

TABLE 3

Test of the Difference in Variability in Running Time between the First Five and Last Five Test Trials for the Experimental and Control Groups and between the Groups at the Beginning and Termination of Test

MEASURE	GROUP			
	E	C	C–E	
	Trials (16–20)–(1–5)	Trials (16–20)–(1–5)	Trials	
			1–5	16–20
t	<1.0	7.24	<1.0	7.56
p	$>.1$	$<.001$	$>.1$	$<.001$

played a great deal of "frustration" behavior—jerky movements, quick dashes and stops, biting of the apparatus, urinating, escape attempts, etc. This behavior appeared to increase in amount as the test trials continued, began earlier in the control group, and occurred less frequently among experimental *S*s.

DISCUSSION

The general conclusion of this investigation is that an irrelevant incentive functions as a learned reward when another primary drive is operating. This conclusion seems warranted by the more rapid and consistent running performance of the experimental *S*s, which encountered the irrelevant incentive in the end box. We would explain the reward value of the irrelevant incentive by its historical and contemporary association with primary reinforcement. Not only have the perceptual properties of the food been coupled with drive reduction in the animal's lifetime, but also in its daily consumption of food in the home cages. The data do not permit any inference as to whether or not stimulation by the irrelevant incentive or the "expectation" of its presence serves to induce a drive, but this is another possible explanatory mechanism.

A crucial issue in this area of research is the completeness of satiation (9). The critic is certain to ask: "But were the animals *really* satiated?" All that can be said in reply is that in only one instance out of 180 opportunities was any consummatory action shown toward the irrelevant incentive. This *S*'s data were discarded whenever they affected the obtained level of significance. And on no occasion were *S*s observed to eat the food provided in their individual handling cages.

Again, the striking incidence of frustration behavior should be stressed. Is such action adequately explained by a fatigue-like reactive inhibition process (4), especially in view of the 24-hr. intertrial interval? If, on the other hand, it is attributed to frustration (1), why are *S*s frustrated in an apparatus where they have never experienced primary reinforcement and presumably have no expectation for such reward? One hypothesis might be that the prolonged privation itself induces a frustration state, which is alleviated partially by the irrelevant incentive. This hypothesis appears somewhat untenable from the results of Wickens and his collaborators (12).

SUMMARY

The purpose of this investigation was to ascertain if the sight of food functions as a secondary reinforcer for thirsty, not-hungry rats. Since the experimental *S*s traversed a runway to food more rapidly and consistently than control *S*s ran to an empty box, it was concluded that learned reward is effective when another primary drive is present.

The reward value of the irrelevant incentive was explained by its historical and contemporary association with primary drive reduction. Whether or not a learned drive was also involved in producing the differential effects

could not be determined by the present experimental design.

The occurrence of intense "emotionality" during the tests was seen as unaccounted for by reactive inhibition or a frustration theory of inhibition. A tentative hypothesis was suggested for this behavior.

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Received February 8, 1954.
Early publication.

THE INFLUENCE OF PREVIOUS EXPERIENCE AND RESIDUAL EFFECTS OF DEPRIVATION ON HOARDING IN THE RAT[1]

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Theories of hoarding behavior differ principally in their interpretation of the origin and motivational basis of the behavior. The instinct theory (7, 8, 10) denies that experience influences hoarding (except for general familiarization with the situation), while the learning theory (2, 4, 5, 6) proposes that the learning process operates to increase the response strength of hoarding. This theory further claims that learning provides the motivational mechanism for the continuation of hoarding when primary motivation is apparently absent during the first few days of satiation following deprivation. The motivation operating during this period is considered to be an externalized drive, as contrasted with the assumption of the instinct theory (8) that the primary motivation continues for a time after restored ad libitum feeding.

The evidence is not yet sufficient to evaluate these theories. Stellar and Morgan (10) demonstrated more hoarding by rats after a deprivation feeding schedule of 18 days than by rats after only 1 day of deprivation when neither group had had previous pellet-carrying experience in the hoarding apparatus. But the increased activity known to occur after the establishment of a feeding cycle (9) may have resulted in more rapid learning by the animals that had long been on the deprivation feeding schedule. At the same time, the evidence for learning found in the early alley activity (4) can be interpreted with ease as being the result of alley familiarization rather than the learning of the hoarding act itself. Some presumptive evidence that hoarding is learned is found in the fact that hoarding is retarded if the animal is not allowed reinforcement in the form of eating after carrying the pellet to the home cage (6), but the animal may merely be learning to eliminate being disturbed by *E*. Clearly, the role of the learning process in hoarding behavior is in need of further investigation.

The present study offers a test of the two hypotheses concerning the origin of the behavior by investigating hoarding in animals when they differ with respect to hoarding experience. The learning theory would predict that experienced rats would hoard more than nonexperienced rats, while the instinct theory would predict no difference with respect to this variable. In addition, the assumption that hoarding scores are influenced by continued primary motivation persisting after 24 hr. of unrestricted feeding is tested by providing different lengths of deprivation immediately prior to this period of feeding.

METHOD

Apparatus

Four batteries of five individual living cages each and a battery of five enclosed hoarding alleys were used; their design was patterned after the one introduced by Hunt (3) and subsequently used in many hoarding studies.

Subjects

Eighteen female albino rats of the Wistar strain were used. They were 145 days of age at the beginning of the experiment, and 195 days of age at the end.

The animals were placed in the individual living cages 35 days before the beginning of the experiment. At this time their diet was changed from the Albers Calf Manna, used in the colony, to Purina Dog Chow in the checker form. This diet was used throughout the experiment.

Ten days before the beginning of the experiment, the animals were assigned to groups by means of a table of random numbers. There were six groups, each containing three rats. The rats were reassigned individual living cages in such a manner that no battery of cages had any group represented by more than one rat.

A light-dark cycle was established 25 days before the beginning of the experiment and held constant thereafter. The lights were on from 6:45 P.M. until

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[1] This paper is based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts at the University of Virginia. The results were also reported to the psychology section of the 1952 meeting of the Virginia Academy of Science. The author wishes to express his gratitude to Dr. Frank W. Finger for his invaluable guidance and generous contribution of time. The writer is also indebted to Dr. Lyne Starling Reid.

7:30 A.M., and off from 7:30 A.M. until 6:45 P.M. On days that hoarding was allowed, the first battery began its 30-min. hoarding session at approximately 9:30 P.M., and the last battery at approximately midnight.

Throughout the experiment, the temperature of the experimental room was maintained at 75° F. ± 1.5°.

Experimental Treatment

The first phase of the experiment was devoted to permitting half the animals to gain hoarding experience while the other half acquired only familiarity with the alley. For 20 consecutive days, each rat was given a 30-min. session with access to the alley. One hundred food checkers had been placed in the alley food bin of each rat that was to be allowed to receive experience, while each rat of the no-experience group found its food bin empty. No food was left in the home cages during the alley sessions in order to encourage the animals to explore, rather than eat, in the cage.

Motivation during this period of the experiment was provided by a deprivation feeding schedule. The rats were deprived for approximately 23 hr. and had food in the home cage for the ½-hr. interval preceding the session with access to the alley. The animals lacking the opportunity to eat in the alley were given a further interval of feeding following the alley session. The length of this interval of feeding was so regulated that their weight losses were equated with the weight losses of the rats receiving experience.

Following this 20-day period the animals were returned to ad libitum feeding until, after 19 days, return to the original body weight was approximately complete for all rats.

During the next three days the second experimental variable was introduced, subdividing the experience and no-experience groups. Six of the rats were placed on complete food deprivation for the full three-day period. Another six were continued on the unrestricted feeding for the first 24 hr., and then placed on complete food deprivation for 48 hr. The remaining six were continued on the ad libitum feeding throughout the three days. Thus, there were six subgroups—three of experience rats that had undergone either 0, 48, or 72 hr. of deprivation (subgroups E_0, E_{48}, and E_{72}), and three of no-experience rats that had undergone either 0, 48, or 72 hr. of deprivation (subgroups N_0, N_{48}, and N_{72}).

After this treatment all the animals were permitted 24 hr. of unrestricted feeding, at the end of which they were given a 30-min. hoarding session. This is the test session for which the theories predict different results. The animals were subsequently continued on ad libitum feeding and tested daily for eight days. At the beginning of each test session, *E* left five food pellets in the home cage.

RESULTS

Effect of Experience

A good indication of the influence of experience is found in the mean for the experience group on test day 1 (28.2 pellets) as compared with the mean for the no-experience group on test day 1 (4.9 pellets). Analysis of variance on a log transformation of the hoarding scores shows this difference to be significant beyond the 1 per cent level of confidence. Furthermore, there are only two cases of overlap between these two groups. One no-experience rat (from subgroup N_0) hoarded 31 pellets, and one experience rat (from subgroup E_0) hoarded none.

It was noted that during the eight test days, five of the animals carried at least one of the five pellets from their home cage onto the alley. An especially interesting case of this "reverse hoarding" is found in the record of the deviant experience rat, which had a hoarding score of zero during the test period. Although this rat did not carry a pellet into the home cage, it was the most frequent "reverse hoarder," carrying all five of its pellets onto the alley on test days 1 and 2. This is more interesting in view of the fact that this rat hoarded during the early part of the training period, but ceased to hoard and began to eat at the food-bin end of the alley during the later part of training. It may be significant for the reinforcement-learning theory of hoarding that it was to this site of eating that the rat carried pellets during the first two test sessions.

A second suggestive observation is found in the distribution of hoarding within a 30-min. session for rats just beginning to hoard. The scores for the single no-experience rat that reached a high level in the first test session clustered largely in the second half of the 30-min. session. The number of pellets carried by this rat in the successive 5-min. intervals was 2, 0, 5, 9, 1, and 14. In the second test session another no-experience rat began hoarding and reached a total of 42 pellets. A similar distribution over the 30-min. session was found for this rat, which, in sucessive 5-min. intervals, hoarded 1, 0, 0, 2, 20, and 19 pellets. In contrast, the scores for the experience rats were distributed evenly over the 30-min. test session on day 1, and dropped off in the latter portion of the session on day 2. This comparison suggests that the gradual rise in hoarding shown by the two no-experience rats represents acquisition of hoarding.

Effect of Deprivation

It became evident in the 20-day training period that the deprivation variable could not be evaluated in the usual manner. During this

TABLE 1

Means and Standard Deviations for Subgroups Differing in Hoarding Experience and Length of Food Deprivation Ending 24 Hr. prior to the Test

GROUP	HOURS OF DEPRIVATION							
	0		48		72		Combined	
	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Experience	16.3	16.5	57.3	3.4	11.0	5.7	28.2	21.8
No experience	11.0	14.2	1.7	2.3	2.0	0.6	4.9	9.4

period the three experience rats, which were later to be deprived for 48 hr., had a daily average of 49.0 pellets as compared with 19.1 for group E_0 and 19.9 for group E_{72}. These three subgroups had, up to this point, been treated exactly alike; therefore, differences between them were simply a result of an unfortunate sampling error. To take these differences into account, the average score for the 20 days of training for each rat was subtracted from its score on the first test day. The resulting scores, then, represent the change in amount of hoarding, with the mean for the 20-day training period taken as the base line. The mean number hoarded by experience rats deprived for 48 hr. increased by 8.3 pellets over their average daily scores made during the training period, while the means for the other two subgroups of experience rats decreased (E_0, 2.8; E_{72}, 8.9). There is no overlap in the difference scores for these three subgroups, and analysis of variance for the log transformation of these difference scores indicates that the null hypothesis may be rejected at the .05 level of confidence.

Because of the dubious validity of the method used in evaluating the influence of deprivation on the hoarding by experienced rats, this portion of the experiment was repeated with 20 *S*s. The second study demonstrated a similar trend, but the results were not statistically significant ($F = 1.199$).

The influence of deprivation upon the hoarding score for the nonexperienced rats can be seen in Table 1. The difference between these subgroups is not statistically significant.

Effect of Continued Feeding and Testing

On successive test days the difference between groups diminishes rapidly. The scores for the experience group dropped on the second test day. The mean for these animals dropped from 28.2 pellets on test day 1 to 9.6 pellets on test day 2. The mean for the no-experience group increased from 4.9 on day 1 to 8.6 on day 2. On the third day hoarding was greatly reduced for both experience and no-experience rats; and from days 4 through 8, the scores had leveled off, with subgroup averages ranging between 3.0 and 0.7 pellets.

DISCUSSION

Earlier experiments provide little basis for choice between the instinct theory and the learning theory of hoarding, since the data are in accord with both. However, of the two, only the learning theory is capable of accounting for the results of the present study. The experienced rats differed from the nonexperienced rats in having had 20 daily 30-min. sessions with the opportunity to hoard. The difference found in the hoarding scores during the first test session can obviously be related to this variable. The low scores of the nonexperienced rats cannot readily be interpreted as the reflection of emotion elicited by strange surroundings since there had been ample opportunity to explore the alleys; nor could the difference be attributed to different degrees of a bodily deficit since the experienced and nonexperienced rats had had equivalent deprivation histories. Clearly, then, the instinct theory, in its present form, is unable to account for this difference in hoarding scores.

The manipulation of the deprivation variable yielded equivocal results. For the experienced rats a trend was observed that suggests that as recent deprivation increases, there is first a rise in performance, and then, as more severe deprivation is used, a drop in performance. But the present study cannot be regarded as definitive on this point. Nevertheless, the literature suggests that primary motivation may persist for more than 24 hr. after restoration of unrestricted feeding. Bahrick (1), for example, has shown in a learning situation that the more severe the preceding deprivation (within the limited range used), the faster is the learning occurring after the animal has been returned to unrestricted feeding. The present study, however, only suggests the possibility of such a persisting primary drive state, without unequivocally demonstrating its reality.

SUMMARY

The present study was designed to determine, first, whether or not learning is a significant factor in hoarding behavior, and, second, whether the motivation for hoarding following recent food deprivation is a persisting primary drive or an acquired externalized drive.

All the *S*s were given access to the hoarding alleys for 20 daily ½-hr. sessions, under 23 hr. of food deprivation. For the experience group there was food in the alley, which permitted acquisition of hoarding experience. For the no-experience group no pellets were placed in the alley, and thus opportunity for learning to manipulate food in the situation was lacking. After recovery from the deprivation feeding cycle, the rats were subjected to either 0, 48, or 72 hr. of total food deprivation. This treatment was immediately followed by 24 hr. of unrestricted feeding after which the animals were tested for hoarding.

The experience group hoarded a significantly greater number of pellets than did the no-experience group, indicating that learning has an important role in hoarding behavior.

No hoarding differences were obtained among the no-experience subgroups with different deprivation histories. Although inconclusive, the results for the experience subgroups suggest residual effects of deprivation on hoarding.

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Received September 23, 1953.

ONE-TRIAL DISCRIMINATION REVERSAL IN THE WHITE RAT

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In a discrimination-reversal experiment, *S* learns a series of discriminations in which the positive and negative stimuli are reversed on successive problems. In the first problem, *S* learns to respond positively to one member of a pair of stimuli to obtain a reward. On the second problem, the other stimulus becomes positive, and *S* learns to respond to it. The execution of a *one-trial* discrimination reversal requires *S* to respond positively to the previously negative stimulus after a single nonreinforced response to the previously positive one.

The purpose of this experiment was to determine whether or not the white rat can learn to make a one-trial discrimination reversal; it was prompted by the fact that the two most pertinent studies of this sort produced contradictory results. Buytendijk's (1) rats showed one-trial reversals after 5 problems or fewer. North (3, 4) was unable to obtain this result in 60 problems. An experiment using procedures different from those of other investigators thus seems in order.

METHOD

Apparatus

The apparatus used in this experiment was the discrimination box developed by Grice (2). It consists of a starting box, a choice compartment, and two food boxes with distinctive patterns. The *S* receives a food reward if it noses open a small metal flap located in the center of the correct food box. In this experiment both food boxes contained food to control for odor cues, and the metal flap on the incorrect box was locked. In order to facilitate learning, the distinctive food boxes remained in the same position throughout the experiment.

Subjects

The *S*s were 9 albino rats, 100 to 140 days old. They were given several days of preliminary habituation in the apparatus in which they learned to get food from each of the food boxes and in which their position preferences were noted. During the experiment they were maintained on a 23-hr. feeding schedule and were fed wet mash at the completion of each experimental session. The reinforcement used in the experiment was a ⅛-in. cube of commercial liverwurst.

Procedure

After habituation, *S*s learned a series of ten *position* discriminations. On the first problem, the *S* was trained against its position preference. When this was learned, the previously negative goal box was made positive for the second problem. The third problem was the same as the first, and so on. Thus, for a rat with a right-position preference, the sequence of correct goal boxes for the ten problems was LRLRLRLRLR.

The *S*s received four trials a day. On each trial the animal was released from the starting box into the choice compartment by raising and then lowering a sliding door. When *S* had taken the food from the correct food box or nosed against the flap of the incorrect one, doors in front of both food boxes were lowered. Correction was not permitted.

Like Buytendijk's, but unlike North's experiment, this one employed a criterion. The problem was reversed when the rat had made 11 out of 12 correct responses, with the last 8 correct. Thus, each problem could be mastered in a minimum of three days. If the criterion was met in the middle of one of the daily four-trial sessions, the problem was not reversed until the following day. It will be noted that, to meet this criterion, the rat had to "remember" the correct response for approximately 24 hr. between daily sessions.

RESULTS

The results of the experiment appear in Figure 1, in which mean number of errors per problem is plotted against the ordinal number of the problem. The rise in the curve between problems 1 and 2 means that, on the first

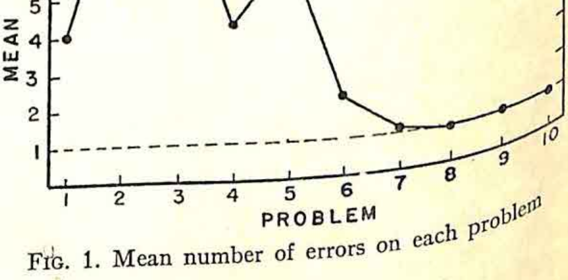

FIG. 1. Mean number of errors on each problem

problem, the position preferences of the rats were not very strong and were easily extinguished. On the second problem, however, the position habit learned in the first problem was strong and difficult to extinguish. Beyond the second problem the curve declines steadily until, on problems 8, 9, and 10, all the rats performed one-trial reversals. One of the most interesting results of the experiment is the remarkable homogeneity of behavior that the animals displayed. The first rat to learn a reversed problem in one trial did so on problem 6; on problem 7 all but one rat produced a one-trial reversal; and on problem 8 all of them showed such behavior.

DISCUSSION

North (3) offers several hypotheses to account for the difference between his results and those of Buytendijk, who also obtained one-trial discrimination reversals in rats. He does not, however, suggest what now seems to us to be the important variable, the use of a criterion of learning. The major suggestion emerging from a comparison of our results with those of North is that the ease of discrimination reversal, at least up to a point, is aided if the original discrimination is well learned. An obvious next step is to study discrimination reversals in a number of independent groups of *S*s that differ in the level of performance required to meet the criterion.

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Received July 25, 1953.

A REPETITION OF THE CALVIN-BICKNELL-SPERLING STUDY OF CONDITIONED DRIVE[1]

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Calvin, Bicknell, and Sperling (1) recently reported a finding that is both startling to the reinforcement theorist and puzzling to the student of hunger. They employed two groups of albino rats, exposing each animal individually to a distinctive environment (a striped box) for 30 min. daily. The animals of one group (high drive) were placed in this environment following 22 hr. of food privation; the animals of the other group (low drive), after 1 hr. of food privation. No animal received food or water in the distinctive environment. Rather, daily rations were administered in the home cages at a much later time. This procedure was repeated until all animals had been given 24 such daily experiences, and then the critical test was introduced. Each animal was food deprived for approximately 11½ hr. (intermediate drive level) and then placed in the distinctive environment with food present. Under these conditions, the food intake of the high-drive group was reliably greater than that of the low-drive group. The authors concluded:

> These results suggest that a previously neutral stimulus situation (the striped box) can acquire motivating properties from association with a relatively strong drive state. These results are interpreted to suggest that reinforcement is not essential for the establishment of a conditioned drive (1, p. 175).

The implications of the Calvin-Bicknell-Sperling experiment are far-reaching. The results are embarrassing to the learning theorist who holds to the principle of reinforcement. They cannot be "squared" with the psychophysiology of hunger. The present study was undertaken with the conviction that the study should be repeated.

METHOD

With little change, we have followed the methodology employed by the original investigators. We shall note any significant variation.

Thirty-two male albino rats of the Sherman strain, varying in age from approximately 150 to 170 days, were utilized as *S*s. At the beginning of the experiment, weights ranged from 208 to 364 gm.

The distinctive environment consisted of a wooden cage of triangular floor plan. The sides were fashioned of ¼-in. plywood panels, 12 in. square. The inside surface of each panel was painted with alternate black and white stripes, approximately ½ in. wide. Top and bottom surfaces consisted of hardware cloth of ½-in. mesh. Illumination was afforded by a single 7-w. bulb suspended about 1 in. above the center of the cage. On the recommendation of one of the previous investigators,[2] the "hurdle," which was used in the original study to further the distinctiveness of the situation, was omitted as superfluous.

Sixteen of these special cages were used. Arranged in nests of four, they occupied an area roughly 2 ft. by 10 ft. During the experiment, each animal was always placed in the same box.

The procedure conveniently breaks down into three stages: adaptation to the feeding cycle, exposure to the unique environment, and the critical test series.

All animals were handled until docile and then placed on a once-daily feeding schedule. Rations consisted of a wet mash of ground Purina Laboratory Chow checkers and water, in the proportion of two to three by weight. The mash was administered daily to all animals in individual home cages, beginning at 6:50 P.M. A large number of food cups and a staggered order of presentation were used. This permitted precise control of the feeding interval. In the original study, the amount of mash presented to the animal was fixed at 25 gm. daily. This provides only 10 gm. of utilizable food (Purina) and was probably calorically insufficient to sustain normal weight. No weights were reported in the original study, but it is our guess that the Calvin-Bicknell-Sperling animals lost weight during the course of the experiment and probably suffered a state of semistarvation in the terminal stages. This should make for some "blurring" of the drive differential between the two groups. To avert this, we fixed the duration of the daily feeding interval rather than the amount of food. Our animals showed a steady and normal weight gain. Our procedure was to present the food mixture for 2 hr. on the first day, 1 hr. on the second, ½ hr. on the third, 15 min. on the fourth and fifth days, 30 min. on the sixth and seventh, and for 20 min. daily thereafter. Daily records of body weight and food intake were taken, and the 20-min. interval was found to be the briefest that permitted normal weight gain. This feeding interval was observed uniformly during the remainder of the experiment.

After 11 days of adaptation to the feeding schedule,

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[1] This research was supported in part by a grant from the Research Committee of the University of Alabama.

[2] Calvin, J. S. Personal communication, 1953.

the box experience was instituted. At this point it was necessary to select the two groups. To insure sensitivity in the final statistical evaluation, it was decided to match the two groups and thus control intragroup variability. The mean daily food intake for the last 4 days of the adaptation period was utilized as a provisional matching criterion. The animals were paired on the basis of this criterion, and one *S* of each pair was randomly assigned to either the high- or the low-drive group. For the 24 subsequent days, each animal of the high-drive group was placed in the box for 30 min. daily, 22 hr. after the daily feeding period. The animals of the low-drive group were placed in the box for 30 min., 1 hr. after their daily feeding period. Again, a staggered schedule was employed, making possible an exact control of all time intervals. In the entire experiment, the margin of error nowhere exceeded one full minute. The high-drive animals occupied the boxes between the clock hours 5:20 and 6:35 P.M.; the low-drive animals, between 8:20 and 9:35 P.M. Body weights were taken every three days, and a steady gain was noted in all animals but one. This animal very soon died.

The first critical test was conducted on the morning of the twenty-fifth day. The animals of both groups were food deprived for 11⅔ hr. Each was then placed in the striped box with a weighed food cup containing the Purina paste. At the end of 10 min., the cup was removed and a second cup immediately substituted. At the end of 20 min., the animal was removed and both cups reweighed. In this fashion, we obtained a record of food intake for the first 10 min. and for the full 20 min. of the test trial. This procedure was repeated on the evening of the twenty-fifth day and on the morning and evening of the twenty-sixth day. During these three trials, a 12-hr. food privation interval was observed.

The original investigators employed food measurement intervals of 5 and 15 min. during the test trials. We elected to use longer intervals to increase reliability.

RESULTS AND DISCUSSION

Table 1 summarizes our findings. During the first and most critical test trial, the mean food intake of the low-drive group ($N = 16$) was found to be slightly greater than that of the high-drive group ($N = 15$) for both the initial 10 min. and for the full 20-min. test interval. A comparison of mean intakes for the entire series of test trials reveals the same slight difference favoring the low-drive group.

TABLE 1

Mean Food Intake in Grams during Test Trials

PERIOD	GROUP		p
	High Drive	Low Drive	
First 10 min. of first test	12.7 ± 5.7	14.2 ± 6.5	$.50 > p > .40$
Full 20 min. of first test	26.6 ± 7.7	28.4 ± 7.9	$> .50$
Total of all four test trials	99.1 ± 18.8	105.3 ± 13.2	$> .50$

It will be recalled that immediately following adaptation to the feeding schedule, our two groups were provisionally matched on the basis of daily food intake. Although there is strong evidence to suggest that the amount of a calorically constant diet that is ingested daily by the rat is unvarying, we re-examined our two groups at the conclusion of the experiment to make assessment of the extent to which they were matched at the time of the critical measurement series. For the four days immediately preceding the critical test series, the mean daily food intake of the low-drive group was found to be 40.3 gm. with a standard deviation of 6.65. The high-drive group yielded a mean of 41.4 with a standard deviation of 5.96. It is apparent that no significant separation of the two groups occurred during the intervening three weeks. At the time of testing, they were well matched with respect to the criterion. Mean daily food intake for the four days preceding the critical tests was found to correlate .538 with the 10-min. intake during the first test, .505 with the full 20-min. intake, and .320 with mean total intake for all four tests.

The slight mean differences favoring the low-drive group, reported in Table 1, were evaluated for significance by employing the t for matched groups. In each instance the standard deviation of the difference was reduced by incorporating one of the above positive correlations into the formula. Each of the obtained t's was less than 1. As the corresponding p values of Table 1 clearly indicate, all our differences may be readily attributed to the operation of chance.

Our findings do not agree with those of Calvin, Bicknell, and Sperling. We can offer no explanation for the disagreement. Strain, age, and weight differences in *S*s and the employment of a test interval of greater duration would seem to constitute inconsequential methodological differences. Our control of daily feeding does represent a significant procedural deviation. But, as noted earlier, by sharpening the drive differential during exposure to the distinctive environment, our operations should make for an even greater separation of the two groups during the critical test series.

SUMMARY

Calvin, Bicknell, and Sperling have reported an experiment that suggests that in the absence of known reinforcement a neutral stimulus situation may take on motivational properties from repeated association with a strong drive state. The present study, a repetition of their experiment, failed to confirm their findings.

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Received September 14, 1953.

DISTINCTIVENESS OF COLOR, FORM, AND POSITION CUES FOR PIGEONS[1]

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In a typical laboratory discrimination learning situation, response to one of a pair of stimuli, the positive stimulus, is reinforced, while response to the other stimulus, the negative stimulus, is not reinforced. An important consideration in discrimination learning is the intrinsic difficulty involved in the recognition of the cue or set of cues that provides the information necessary for the appropriate discrimination of the positive from the negative stimulus. In order to be able to learn to discriminate two stimuli, an organism must first be capable of perceiving the relevant cue dimension (e.g., color, form, position) and also must be able to recognize the difference in that cue dimension which distinguishes the positive from the negative cue. The comparative ease of this twofold perceptual process shall be considered a reflection of the relative "distinctiveness" of the cues involved.

Where members of a stimulus pair differ from each other with respect to more than one cue dimension, any one or any combination of the cues may serve the *S* as a basis for discrimination. Such an ambiguous-cue problem is that initially presented to *S*s of the present study, wherein pairs of stimuli differ with respect to position (right vs. left stimulus card), form (circle vs. triangle), and color (green vs. red stimulus card). The procedure is designed to determine the relative distinctiveness of these three sets of cues for pigeons.

As a check of the results of performance in this initial investigation, the same *S*s are subsequently tested for speed of learning on discrimination problems for which the solution is dictated by *E* to be the discrimination of position, form, *or* color cues.

The one reported study attempting to define the relative difficulty of various sensory discrimination learning problems in pigeons, that of Rouse (4) in 1906, is one that suffers from lack of control of experimental conditions. The most notable defect in the design is the uniform order of presentation of problems. For all *S*s, position discrimination training was initially presented, followed by color training, and finally by form training. The obtained results (Rouse reported a gradient of difficulty from position discrimination through color discrimination to form discrimination, from the easiest to the most difficult problems) might be attributable either to interference of earlier learned response habits or to real differences in difficulty of problems.

Studies in this area, using *S*s other than pigeons, provide conflicting results. For example, results of studies comparing the difficulty of form discrimination and color discrimination in anthropoid *S*s have been notably inconsistent. Early investigations suggest that monkeys are able to associate food with forms more readily than with colors (8, pp. 375–376), while a number of more recent studies have indicated that, for the monkey, color discrimination is easier than form discrimination (e.g., 1).

In surveying findings concerning the relative difficulty of position, form, and color discrimination, one discovers not only results differing for animals of different species, but also a disparity of results for animals within particular species. Further, such studies supply results derived from only certain limited ranges of the various stimulus dimensions investigated. Certain forms are arbitrarily chosen from an infinite number of possible form stimuli; the colors presented the experimental *S*s far from exhaust the possible different colors available for use. In addition, it has not been possible to scale the stimulus dimensions so as to enable presentation of pairs of form stimuli and pairs of color stimuli for which the discriminative differences may be assumed to be equal. In view of these restrictions, results must be viewed in relation to the conditions imposed in each study. Generalization of conclusions, even within a particular species, is severely limited.

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[1] This paper is based upon a portion of a dissertation submitted to the Department of Psychology, Stanford University, in partial fulfillment of the requirements for the Ph.D. degree. The writer is indebted to Dr. Douglas H. Lawrence, Dr. Calvin P. Stone, and Dr. Ernest R. Hilgard for their invaluable guidance throughout the course of the study.

METHOD

Subjects

Six experimentally naive Silver King pigeons, three male and three female, served as *S*s. While all were over two years old, their exact ages were unknown. All *S*s had been living in laboratory cages for a period of at least four weeks before the onset of training. During this period each *S* received a daily food ration of from 10 to 16 gm. of mixed-grain pigeon feed, the exact amount determined so as to stabilize the *S*'s weight at a level between 75 and 80 per cent of its weight under free-feeding conditions. Water and grit were available to the birds at all times in containers affixed to the rear wall of each cage.

Apparatus

Each *S* was housed in a modified Skinner box, 26 by 30 in., 22 in. high, which served both as living cage and experimental box. Three sides of the cage were plywood, the fourth was glass, and the top and bottom were chicken wire. On the floor of the cage, centered, was a small, wooden roosting block. On the right side of the cage, as viewed from the glass front, was a retractible food tray, 1½ in. from the floor of the cage. Two plastic containers, for water and for grit, were attached to the rear wall 3 in. from the floor of the cage and within 8 in. of the right wall. On the left side of the cage a 3-in. strip was cut out from the wall, parallel to the floor, providing for the presentation of stimulus cards. The base of this stimulus panel was 4½ in. from the floor; sheet metal strips inserted in the panel served as shutters in front of the stimulus cards. The shutters were kept fully closed except during training sessions.

Stimulus cards consist of: (*a*) a 3-in.-square gray card of Munsell (9) brightness value 7; (*b*) a "strong" red equilateral triangle of brightness value 4, area 2.9 sq. in., cemented to a 3-in.-square white background card; (*c*) a "strong" green triangle, brightness value 6, of the same area, cemented to an identical background card; (*d*) a red circle, area of 2.9 sq. in., cemented to a 3-in.-square white background card; and (*e*) a green circle of the same area affixed to an identical background card. All stimulus cards were cemented to a plywood board designed to slide into the stimulus panel of the Skinner box.

The only light sources in the experimental room were frosted skylights, located centrally so that light was approximately equal in all experimental cages. Trials were run at intervals of 24 hr. (never less than 23 or more than 25) in mid-afternoon, so that light conditions varied only slightly from day to day.

Procedure

Preliminary training. Since all *S*s were experimentally naive, it was necessary to include preliminary training sessions in order that the birds would learn to peck at the stimulus cards. The method employed was that which Skinner called the method of successive approximation (5, p. 339). The *S* was first trained to orient toward the left side of the cage, then to peck at a stick near the left wall of the cage, and, finally, to transfer the pecking response from the stick to the neutral gray stimulus card. This change in behavior was effected by rewarding the various sequences of responses with a few grains of feed. All *S*s mastered the final card-pecking response within nine days of training, or 225 trials.

Experimental training. A "correction" method was used during all experimental training trials. The *S* was permitted to consume between six and eight grains of food immediately after each correct response. A response consisted of a pecking movement resulting in contact of the bill with one or the other stimulus card.

Two *E*s were present during each experimental session. One presented the stimulus cards and rewards, and controlled the switch of the time clock; the other recorded the time and error scores for each trial.

On the day following mastery of the response to the gray stimulus card in preliminary training, each *S* was given 25 trials with the red triangle to the left and the green circle to the right. A peck at the green circle was rewarded. Solution of this problem was possible on the basis of greenness, circularity, or right position on the stimulus panel. On each succeeding day, 25 trials were given until each *S* responded without error for ten successive trials.

After meeting this criterion, each *S* was given one day of test trials to determine which of the three possible cues was the basis for the acquired discrimination. Of the possible 16 pairs of stimuli, including different combinations of color, form, and position, 4 were chosen for the test trials (Table 1). These 4 patterns are the only ones which exhibit each of the six cues (red, green, circle, triangle, right, left) once and only once in every pairing. There are two advantages in utilizing these 4 patterns: (*a*) *S*s are never faced with an insoluble problem during the test series, and (*b*) each of the 4 patterns chosen exhibits *all* cues exactly once, so that, in a series of trials, each cue is presented the same number of times. The *S* is forced to respond to red *or* green, circle *or* triangle, and right *or* left on each trial.

The test day includes 5 initial trials identical to those of the preceding training session, followed by 16 test trials, 4 trials with each of the pairs shown in Table 1. These trials were presented randomly with the restriction that no pattern was presented twice on successive trials. During this test series there were no wrong responses; each peck was rewarded with six to eight grains of food.

Following the day of test trials, each *S* was assigned three discrimination problems: one based upon position, one upon form, and one upon color, as outlined in Table 2. Each *S* was presented the problems in one of the six possible orders. The *S*s were presented the four stimulus patterns of Table 1 in random order, with the restriction that each pattern was offered six times during each day's series of 24 trials. Reinforcement was given for a peck to the right card in the position problem, to the circle in the form problem, and to the green card in the color problem.

RESULTS AND DISCUSSION

Initial Discrimination Training

In Table 3 are displayed the data for ambiguous-cue training trials. The number of trials to the criterion of ten successive correct responses varies between 11 and 42. Comparable variability is shown in the number of trials on which *S*'s initial peck was to the "wrong" stimulus card ("error" trials), in the total number of wrong pecks, and in the median time per trial.

Discrimination Test Trials

On the first 5 trials of the discrimination test period, trials for which stimuli presented were identical to those of the previous day's training trials, no *S* made an error. Results for the 16 subsequent critical trials are given in Table 4, which lists the number of observed responses of each *S* to each of the four pairs of stimuli described in Table 1.

The results indicate a close correspondence between observed patterns of response and those predicted on the basis of a hypothesis of perceptual dominance of a particular cue. Four *S*s (*A*, *B*, *E*, and *F*) responded consistently to the green cue, irrespective of position or form, while two *S*s (*C* and *D*) responded consistently to the stimulus of right position, regardless of form or color. This correspondence was perfect for *S*s *C* and *F*. No bird's actual responses differed on more than 2 of the 16 trials from responses expected (i.e., from a consistent pattern, with respect to either color or position). Analysis of scores on the discrimination training problem (Table 3) suggests no explanative differences between those pigeons responding to color and those responding to position on the critical test trials.

TABLE 1

Stimulus Patterns Presented on Test Trials

PATTERN NO.	LEFT STIMULUS	RIGHT STIMULUS
1	Red triangle	Green circle
2	Green triangle	Red circle
3	Green circle	Red triangle
4	Red circle	Green triangle

TABLE 2

Order of Presentation: Final Discrimination Problems

S	DISCRIMINATION PROBLEM		
	Position	Form	Color
A	1	2	3
B	3	1	2
C	3	2	1
D	2	3	1
E	2	1	3
F	1	3	2

TABLE 3

Results of Ambiguous-Cue Training

S	SEX	TRIALS TO CRITERION	TOTAL ERROR TRIALS	TOTAL ERROR PECKS	MDN TIME PER TRIAL (SEC.)
A	M	39	22	68	3.0
B	F	42	18	48	3.1
C	M	11	8	18	2.6
D	F	38	26	182	3.4
E	M	31	8	34	2.1
F	F	24	12	53	2.0

TABLE 4

Observed Responses on Discrimination Test Trials

STIMULI	SUBJECT					
	A	*B*	*C*	*D*	*E*	*F*
L. Red triangle	0	1	0	0	0	0
R. Green circle	4	3	4	4	4	4
L. Green triangle	3	4	0	0	3	4
R. Red circle	1	0	4	4	1	0
L. Green circle	4	4	0	1	3	4
R. Red triangle	0	0	4	3	1	0
L. Red circle	0	1	0	0	0	0
R. Green triangle	4	3	4	4	4	4

Final Discrimination Problems

The experimental design for the series of final discrimination problems (Table 2) provides opportunity for the transfer of learning from one problem to the next, and it is possible to analyze the extent to which responses appropriate to a particular problem dominate the errors that occur on a subsequent problem. We shall refer to error pecks that would have served as correct responses on the previously presented discrimination problem as perseverative errors.

It is assumed that learning of discrimination on each of the three problems presented in this experiment progresses, in continuous fashion, through three stages: (*a*) persisting response to the relevant cue of the previous problem, (*b*) perception of, and extra-chance response to, the new relevant cue, and (*c*) ex-

TABLE 5

Results on Final Discrimination Problems

S	TRIALS TO CRITERION			ERROR TRIALS			TOTAL ERROR PECKS			NONPERSEVERATIVE ERROR PECKS		
	Color	Pos.	Form	Color	Pos.	Form	Color	Pos.	Form	Color	Pos.	Form
A	55	193	199	22	63	62	100	199	234	13	14	66
B	106	34	121	30	15	49	46	30	205	19	2	36
C	78	59	121	19	11	37	68	73	222	1	0	13
D	112	25	319	28	4	115	92	19	465	2	0	114
E	90	222	237	25	56	97	119	97	310	23	15	73
F	39	27	73	8	10	26	33	108	182	1	2	14
Total	480	560	1070	132	159	386	458	526	1618	59	33	316
Mean	80.0	93.3	178.3	22.0	26.5	64.3	76.3	87.7	269.7	9.8	5.5	52.7

clusive response on the basis of that new cue. Perseverative errors would be expected to appear on about one-half of the trials during the first, presolution stage of learning, since the perseverative response differs from the new correct response on half the trials. With the onset of the second stage, perseverative errors would be expected to decrease, and at the third stage they would disappear. At no time would we expect to find nonperseverative errors if the new cue were a perceptually potent or distinctive one. Nonperseverative errors would arise only if *S*s failed to respond readily to the new cue. On the basis of this formulation, the mean number of nonperseverative errors for each problem will be inversely related to the distinctiveness of the cues relevant to solution.

Four sets of related performance scores—number of trials to a criterion of ten successive errorless trials, number of trials on which at least one error preceded correct response, total number of error pecks, and number of nonperseverative error pecks—are presented in Table 5. Since tests upon scores in the columns of Table 5 provide evidence for heterogeneous variances, application of analysis of variance is not legitimate. Alternative nonparametric tests serve to demonstrate consistent and statistically significant performance differences related to the dimensions of the discrimination cues. Results support the contention that association of response with form cues is more difficult for the *S*s than is association of response with either position or color cues. In particular, the striking differences among nonperseverative error peck scores for the three problems tend to confirm the hypothesis that the relative distinctiveness of color and position cues, as contrasted with form, is chiefly responsible for obtained differences in ease of discrimination learning.

Since, in the present study, brightness values for red and green stimuli were not identical, it remains to consider the possibility that *S*s were responding not to differences in hue, as has been assumed, but to brightness differences. The prepotency of hue over brightness has been repeatedly demonstrated for chicks (8, pp. 197–200). That differences in brightness of colored stimuli are irrelevant to the solution of color discrimination problems for the pigeons of the present study is demonstrated by an auxiliary investigation. After relearning the color discrimination problem, each *S* was presented with 16 trials on which brightness values of red and green stimulus cards were reversed; for no *S* was the color discrimination habit disrupted.

While the present study definitely suggests a greater difficulty in form discrimination than in either position or color discrimination, it has failed to demonstrate consistent differences in favor either of position or of color discrimination problems. This may surprise some animal experimenters, such as Spence, who states: "Position habits, to the right or left, represent by far the most common systematic responses made by animals when first introduced to the discrimination problem" (6, p. 439). It seems likely that pigeons (and probably most other birds) throughout their life spans utilize color cues to a greater extent than most other animals. Thorndike's early study (7), demonstrating pecking responses to colored stimulus patches in the one-day-old chick, suggests that some form of color discrimination is innate in the chick. Recent work of Gogel and Hess (2) is corroboratory. Lawrence (3) has reported that a cue may acquire distinctiveness in the course of experience. Experience of the mature pigeon, in selection of grain food and in recognition of threat in the form of enemy birds, may have enhanced the distinctiveness of color as a cue.

Results of the present study provide a direct contrast to a number of earlier reports that pigeons do not perform consistently when used as laboratory *S*s (e.g., 8, p. 247). It would appear that if appropriate motivation is maintained, if *S*s are sufficiently handled and tamed by *E*, if *S*s are thoroughly familiar with experimental cages, and if the response required of the birds is an appropriate pigeon response, then the pigeon is a consistent and hard-working laboratory animal.

SUMMARY

Six experimentally naive pigeons were trained by the method of successive approximation to peck a stimulus card when the card was presented in the experimental cage. They then were subjected to an ambiguous-cue discrimination problem in which the three stimulus dimensions were color (green vs. red), form (circle vs. triangle), and position (right vs. left). After discrimination had been exhibited, a test was made to determine the stimulus dimensions that had served as relevant cues. This test revealed each *S* to be responding consistently to one of the three dimensions. Four of the *S*s were responding to color, while the other two *S*s were responding to the position of stimulus cards.

In subsequent discrimination training, the same *S*s were presented successively three problems, in each of which a response to one of the stimulus aspects—color, form, or position—was essential to successful solution. Learning of the form discrimination was consistently the most difficult; the group data show no consistent differences between color and position discrimination learning.

Results are viewed as lending support to the importance of relative distinctiveness of cues as a determinant of ease in discrimination learning. For the pigeons of the present study, form cues are less distinctive than either color or position cues.

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Received July 31, 1953.

PERSISTENCE OF VISUAL EXPLORATION IN MONKEYS[1]

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The present experiments were designed to determine the strength of visual exploration in monkeys. The apparatus and general method have been previously described by Butler (2). Visual exploration response strength was tested by two methods, one measuring the effect on response latency of continuous testing over 4-hr. periods, the other determining the maximal period of responsiveness under conditions of continual testing. These satiation tests were carried out on both normal and brain-damaged monkeys, but individual differences in experience and age make it impossible to draw more than highly tenuous conclusions concerning the effects of operative state.

METHOD

Subjects

Six adult rhesus monkeys (No. 102, 129, 130, 147, 158, and 222) served as *S*s in Experiment I, and seven adult rhesus monkeys (No. 156, 159, 167, 129, 130, 147, and 158) were *S*s in Experiment II. The overlapping *S*s were tested in Experiment I first and in Experiment II subsequently. Animals 102, 156, 159, and 167 were normal monkeys. Animals 129 and 130 had undergone bilateral extirpation of the prefrontal areas and are subsequently called prefrontal monkeys. Monkey 158 had been subjected to nearly total bilateral extirpation of the temporal neocortex when first tested, and animal 147 was originally tested as a normal *S* and subsequently tested after nearly total bilateral extirpation of the temporal neocortex. Numbers 158 and 147 are postoperatively described as temporal animals. Number 222 (amygdaloid monkey) was subjected to an operation that was designed to ablate the amygdaloid nuclei completely and additionally involved bilateral damage to the ventral tip of the temporal lobes. The extent of the lesions, as estimated at the time of surgery, is indicated in Figure 1.[2] All the monkeys except No. 222 had had previous training on food-rewarded problems, ranging from approximately two years' test experience for No. 167 to eight years' experience for No. 102. Prior to the present experiments, monkeys No. 102, 129, 130, 147, 156, and 159 had been *S*s on manipulation drive studies, and No. 156, 159, and 167 had been tested on discrimination learning to visual exploration motivation. Number 222 had had no previous test experience.

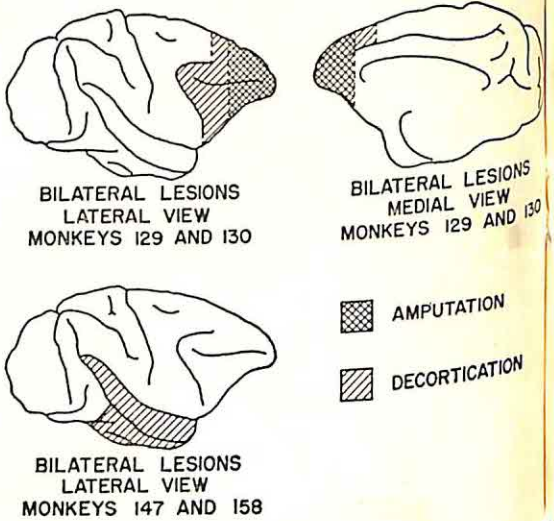

FIG. 1. Localization of lesions

Apparatus

The apparatus (Fig. 2) consisted of a wire cage measuring 27 in. by 17 in. by 26 in. Over this cage, *E* placed a box with a Masonite top and front and with heavy black cloth covering the back and sides. Illumination was provided from within by a 25-w. lamp. Two doors 3¾ in. by 4 in. were fastened flush to the front of the box. Each door could be locked by a wooden pin containing a leaf switch connected to a 6-v. battery. Pressure against a locked door activated this leaf switch, illuminating a signal light attached to the front of the apparatus. A transparent Lucite plate fixed to the inside face of each door permitted insertion of 3-in. square, colored stimulus cards between the plate and door. An opaque screen, which could be raised or lowered by *E*, separated the colored cards from the animals.

The apparatus was placed in the entrance room of the Wisconsin Primate Laboratory. Temperatures in the test room ranged from 69° to 79° F. and averaged 72.5° F. during Experiment I. In the second experiment, temperatures ranged from 69° to 82° F., averaging 75.4° F. Temperature in the test cage increased approximately 6° above test room temperature during a 4-hr. test session.

Procedure

Preliminary training. The *S*s in Experiment I were placed in the apparatus for 5 min. before preliminary

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[1] These researches were supported in part by a grant to the University of Wisconsin from the Atomic Energy Commission Contract No. AT(11–1)–64 and in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

[2] Detailed descriptions of the operations and operative procedures will be made available upon request.

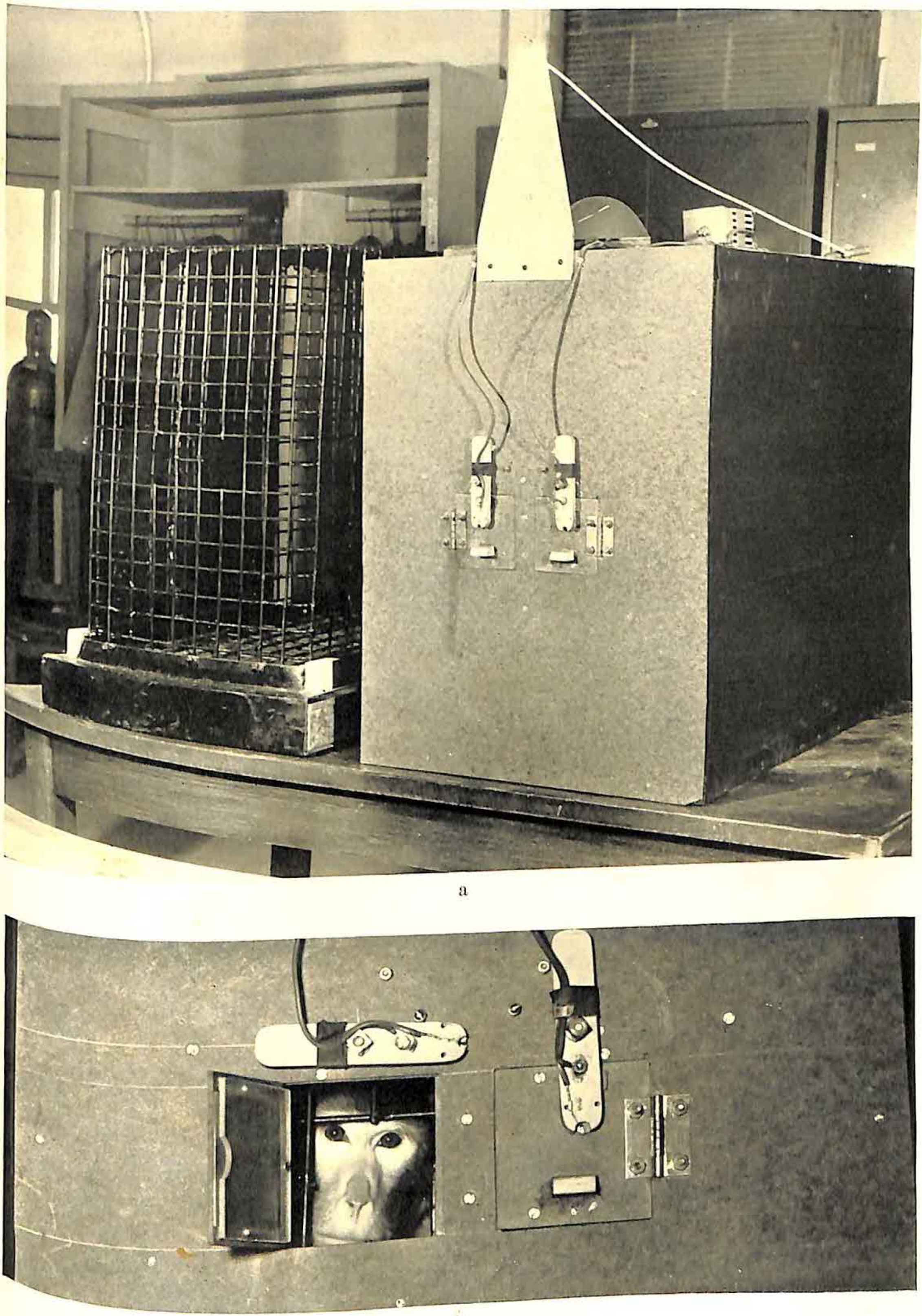

FIG. 2. Visual exploration apparatus (two views)

training trials began, and both doors, neither holding a stimulus card, were closed. One door was always locked, the position of the locked door following a predetermined order balanced for frequency. The *E* initiated a trial by raising the opaque screen, thereby exposing the doors to the animals. If *S* pushed against and opened the unlocked door, it was allowed 30 sec. to explore the environment visually before *E* lowered the opaque screen and ended the trial. If the monkey failed to open the unlocked door within 5 min., *E* opened it from the outside and waited 30 sec. before lowering the screen. Intertrial interval, defined as time between lowering and raising the opaque screen, was 30 sec. Preliminary training consisted of 20 trials a day for two days.

In Experiment II, the operated monkeys No. 129, 130, 147, and 158 had been *S*s in the first experiment, and the normal controls No. 156, 159, and 167 had been tested previously on a series of discrimination learning problems in the visual exploration apparatus. No preliminary training was given in the visual exploration apparatus.

Discrimination training. In Experiment I, colored stimulus cards were inserted between the Lucite plate and the inside face of each door. The *E* started a trial by raising the opaque screen, thus presenting the stimulus cards to the animals. If *S* pushed against the door containing the positive stimulus card, the door opened and the animal was permitted 30 sec. to view the environment, which consisted of the entrance room of the laboratory and the activities occurring within it. At the end of this interval, *E* lowered the screen. If *S* pushed against the door containing the negative stimulus card, the door engaged the locking device and illuminated the signal light on the front of the apparatus. The *E* immediately lowered the screen, thereby preventing *S* from opening the other door. If *S* failed to respond to a door within 5 min., *E* opened the correct door from the outside, permitting *S* to explore for 30 sec., and then ended the trial by lowering the screen. The position of the stimulus cards was changed from trial to trial in a systematic order with positions balanced for frequency. The intertrial interval was 30 sec., during which the stimulus cards were either rearranged or removed and returned to their previous position. A noncorrection technique was used throughout.

The normal and the prefrontal monkeys were tested on a yellow-blue color discrimination, with yellow positive for No. 147 and 130, and blue positive for No. 102 and 129. A red-green discrimination problem was given to the temporal lobe monkeys because No. 147 had been preoperatively tested on yellow vs. blue. Red was positive for No. 147 and green was positive for No. 158. Number 222 was also tested on the red-green discrimination, with green positive.

The *S*s were tested four continuous hours a day for five days. The total number of trials was a function of each monkey's particular responsiveness. Laboratory schedules prevented the establishment of comparable testing schedules for all animals. A day's rest was interposed between days 3 and 4 for the normal and prefrontal monkeys, and the testing of the temporal lobe monkeys and the amygdaloid monkey was interrupted one day between days 1 and 2.

The amygdaloid monkey was given one additional 4-hr. day of testing during which it received visual rewards during hours 1 and 4 and combined visual and food rewards during hours 2 and 3. This additional testing was designed to determine whether or not *S*'s performance, which was at a low level, would be facilitated by the addition of food.

Correct responses and response latencies, defined as the time between *E*'s raising the opaque screen and *S*'s response to a door, were recorded. In addition, records were kept of cage shaking, vocalization, defecation, and urination.

Trial procedures in Experiment II were the same as those described for Experiment I. Orange and gray stimulus cards were used, the orange card being correct for monkeys No. 130, 156, and 158, and the gray card for monkeys No. 129, 147, 159, and 167.

The *S*s were tested until they either failed to respond within 5 min. on two successive trials or failed to respond within 5 min. on three of five consecutive trials.

Testing began between 9:00 and 10:00 A.M., approximately 1 hr. after the animals had been fed a standard laboratory meal and their water bottles refilled. Because of the hyperactivity of the prefrontal monkeys and consequent danger of dehydration, a metal tray containing water was fixed to the floor of the test apparatus during Experiment II.

During both experiments, visual and auditory environmental stimulation varied greatly, because many different laboratory activities routinely occurred in the room where the test apparatus was located. Precautions were taken, however, to prevent *S*s from seeing food or other monkeys.

RESULTS

Experiment I

The data of Figure 3, in which mean log latencies on successive test days are presented, give no indication of any satiation effect. No significant increase in latency is disclosed by

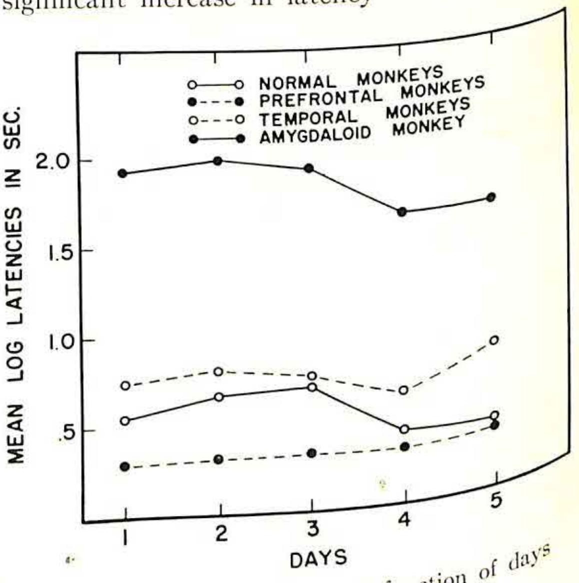

Fig. 3. Response latencies as a function of days

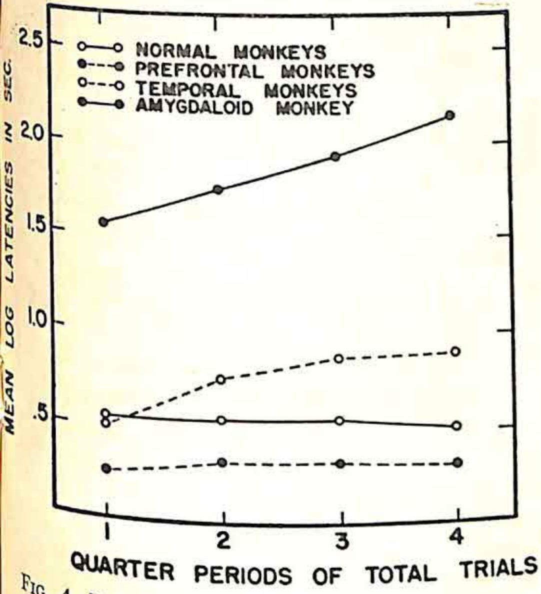

FIG. 4. Response latencies within test periods

comparing any pair of successive days or by comparing day 1 and day 5 performances. Indeed, the most striking changes in performance, those made by the normal monkeys and the amygdaloid animal, show a decrease rather than an increase in mean log latency when days 1 and 5 are compared.

Similar results obtain in Figure 4 for the normal and prefrontal monkeys when latencies on successive quarters of trials within days are measured. The one amygdaloid and two temporal monkeys did, however, demonstrate increasing latencies of response for the within-day periods, and this increase is regular and progressive for the amygdaloid animal. All the normal and prefrontal monkeys gave evidence of learning the discrimination problem (see Fig. 5), and their performances are significantly better than chance on each of the last six blocks of 100 trials. All these animals, except No. 147, attained a consistently high level of efficiency. Neither temporal monkey demonstrated any evidence of learning. The amygdaloid animal, whose responses are not plotted on the figure because of the small number of trials, made 54, 52, 56, and 60 per cent correct responses on successive blocks of 50 trials, a performance which fails on every block of trials to obtain significance at the .05 level. This animal on the additional day of testing had a mean response latency of 72 sec. when rewarded by visual exploration only, compared with 3 sec. when a food incentive was added. On day 6, No. 222 had 61 per cent correct responses to visual exploration alone (44 trials), and 69 per cent responses to visual exploration plus food (108 trials).

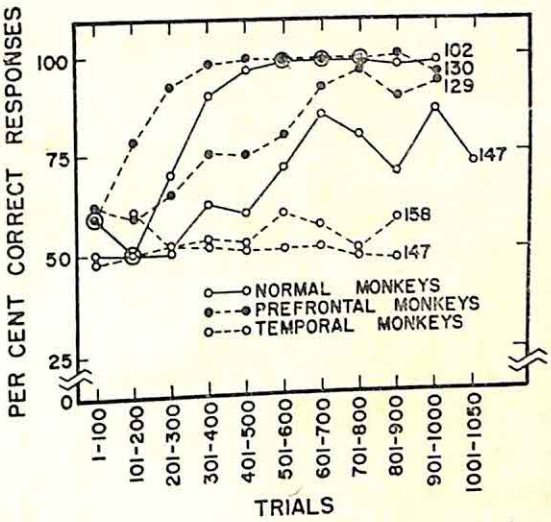

FIG. 5. Discrimination learning to visual incentives

Experiment II

As is shown in Figure 6, the three normal monkeys responded, respectively, 9, 11, and 19 hr. before satiation took place; the two frontal monkeys became satiated in 11.5 and 12 hr.; and the temporal monkeys failed to respond after 5.5 and 11 hr. The total number of responses made by the seven *S*s were 325, 612, 775, 634, 698, 241, and 357 for monkeys 167, 159, 156, 130, 129, 147, and 158, respectively. Although the small number of cases precludes the possibility of statistical comparisons among the groups, the extremely short latencies maintained by the two frontal monkeys throughout a 10-hr. period is noteworthy. The most striking result found in this experiment is, of course, the extreme resistance to satiation.

One normal and both prefrontal monkeys responded to the correct object at a level significantly beyond chance for several hundred successive trials. In the case of one prefrontal animal, No. 130, this could be interpreted as a color preference, but the other animals, No. 156 and 129, clearly demonstrated learning, because a statistically significant difference existed between performance on the first

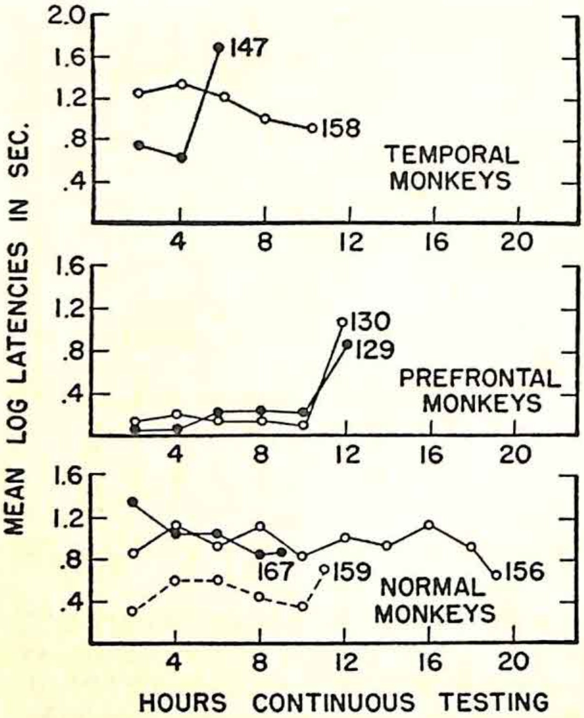

FIG. 6. Response latencies as a function of hours of continuous testing

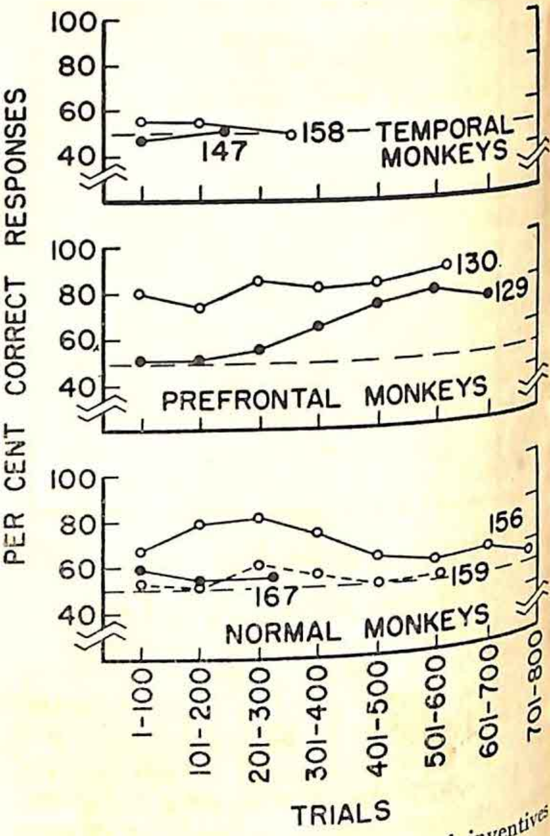

FIG. 7. Discrimination learning to visual inventives

hundred and on some subsequent hundreds of trials (see Fig. 7).

Observational Data

All three animals with temporal lesions were observed by *E* to be asleep at the end of the allotted 5-min. response interval. During Experiment I, monkeys 147, 158, and 222 were observed to be sleeping 1, 29, and 20 different times, respectively. During Experiment II, No. 158 was observed to be sleeping at the end of five different response intervals, two of which occurred in succession and automatically ended the satiation test session. No normal or frontal monkey was observed to be asleep at the end of a response interval.

Both prefrontal monkeys were hyperactive, and this hyperactivity appears to have influenced their mean response time. These monkeys circled about the cage continuously, passing the doors about once a second. Pushing against the door appeared to be part of the activity sequence, for the monkeys rarely interrupted their circling to view the environment outside the test apparatus. Occasionally they would stop pacing for several seconds when an *E* moved toward or away from the apparatus, but usually the monkeys would look through the open door only as they passed by. In spite of the cursory nature of their visual exploratory responses, the data show that these two animals learned as rapidly and subsequently performed as efficiently as the normal monkeys.

DISCUSSION

The data of the present experiments demonstrate in a very striking manner the resistance of visual exploration responses to satiation. Normal (and prefrontal) monkeys demonstrate no tendency toward increased latencies of visual exploration responses either during 4-hr. continuous test sessions within days, or between days. For the normal monkeys, the mean latencies actually decrease from day 3 to days 4 and 5. Latencies did not appear to be confounded with learning, for there was no consistent increase or decrease in mean daily response time corresponding to the continued increases in percentage of correct responses recorded for the normal and prefrontal monkeys.

These data make it appear unlikely that visual exploration can be explained as a derived drive based on some so-called primary drive such as hunger, thirst, or sex. If visual exploration were so determined, one would expect the second-order drive to become extinguished following persistent failure of reinforcement of the primary drive. The fact that no such extinction takes place argues strongly against its interpretation as a derived drive.

The results of the satiation experiments further support the view that visual exploration is not a derived drive, for visual exploratory responses in normal and prefrontal animals continued for periods of from 9.5 to 19 hr. (mean = 12.3 hr.) during which 325 to 775 responses were made (mean = 609 responses). Furthermore, drive strength, as measured by mean log latency of response, frequently held constant or even increased for very long periods of time.

Explanation of visual exploratory responsiveness in terms of anxiety seems unlikely in view of the lack of evidence of behavioral disturbance in the experimental situation. Observation of urination, defecation, vocalization, and cage shaking gave no indication that these evidences of disturbance were any more frequent in the test apparatus than in the home cages. The relationship of visual exploration to these behaviors and the effects of parameters of age, test adaptation, and various past experiences remain to be disclosed.

The authors interpret the visual exploration responses as belonging to a broad category of curiosity of exploratory drives that are elicited by external stimuli and include the manipulation drives previously described in the Wisconsin Laboratory (4, 5, 6) and probably include similar exteroceptively elicited drives described for subprimate animals (1, 3, 7, 8, 9, 10).

The data presented in the present experiment comparing performance of normal monkeys and those with cortical lesions suggest that temporal lobe lesions either directly or indirectly depress visual exploratory drive, and the prefrontal lesions increase general activity without otherwise changing visual exploratory responsiveness in any significant manner.

CONCLUSIONS

1. Two experiments were designed to study the persistence of visual exploration in normal and brain-operated monkeys. Experiment I involved testing six animals four continuous hours a day for five days on a color discrimination problem in which the only reward was that provided by visual exploration of the surrounding environment. In Experiment II, seven animals were tested for one continuous session on a similar discrimination problem until they ceased responding to visual incentives.

2. The motivational mechanism underlying performance is interpreted as being that of visual exploration, which, in addition to serving as a basis for discrimination learning, is extremely resistant to satiation.

3. The data suggested that visual exploration motivation is depressed in monkeys with bilateral damage to the temporal lobes.

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Received September 17, 1953.

PUPILLARY CONTRACTION AND DILATION IN LIGHT AND DARKNESS[1]

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Pupillary contraction and dilation have been studied by a number of investigators, who used techniques ranging from intermittent measurement with a pupillometer or with a camera (1, 2, 3, 9, 11), through white-light motion picture photography for contraction and single repeated flash photography for dilation (4, 5, 7, 10), to high-speed infrared photography which permits taking as many as 50 pictures per second (6). The variety of methods and purposes involved in these studies has yielded widely different values for the latency of pupil contraction and dilation. The latency of pupillary response to light after prior darkness has been variously given as .187 sec. (4), .20 to .28 sec. (6), .217 sec. (7), or longer (ranging from ⅓ to ½ sec. [1]). Reeves (10) describes the contraction to 100 mL. as reaching minimal size in less than 5 sec., with a greater part of the constriction occurring within the first 2 sec. Gradle (4) describes a rapid primary contraction for .4365 sec. at the rate of 5.48 mm. per second; this is followed by a secondary contraction of .3125 sec. at the slower rate of 1.34 mm. per second. Lowenstein describes the contraction as beginning with a rapid movement, which slows down after .2 to .3 sec.

The latency of the pupillary response to darkness after prior adaptation of the eye to light has been described as equal to or longer than that for contraction (6) or as being without a latent period (4). Gradle (4) describes the dilation from prior adaptation to an 8-amp. arc light as proceeding at the rate of .95 mm. per second. Reeves states that the average pupil requires 5 min. to reach its maximum diameter from adaptation to 100 mL. In Reeves's study the average dilation at 9 sec. for six *S*s was 74 per cent of the maximum reached at the longer time of 5 min.

This study seeks to determine values for the contraction and dilation latencies, the nature of the contraction and dilation curves, and some of the conditions under which these vary.

METHOD

Apparatus

The study used infrared photography with an apparatus that has been described elsewhere (12). The illuminated field to which the pupil constricted was a uniform, diffuse round spot 4.7 cm. in diameter, with a luminance of 8,800 mL. This spot was mounted 15 cm. from the eye, with the center of the spot at an angle of 20° below the line of regard, thus illuminating both eyes although only the right eye was photographed. In the first experiment the spot was covered by an Ilex shutter controlled by a solenoid wired into the timing circuit. The operation of the solenoid constituted the only noise in the experimental situation; this noise was effectively eliminated by putting cotton in *S*s' ears and placing earphones over their ears. The shutter was not used in the second experiment since the contraction light was wired directly into one of the timers, which were located in a separate room. The onset and duration of the visible illumination are recorded on the film strip by an over-all darkening of the film without obscuring the individual pictures of the pupil. A small mirror was placed above the illuminated field and 7° below the horizontal. By means of this mirror, *S* fixated a very low-luminance red target, consisting of a series of concentric circles, the largest of which was 19 mm. in diameter. The total distance from the eye to the circles was 1 m.

Subjects

Ten *S*s were used in the first part of this study, seven male and three female, ranging in age from 21 to 29 years. All had normal or nearly normal refraction and light-colored irides. Five of the same *S*s were used in the second part of the study.

Procedure

The *S* was seated in such a manner that he could keep a bite board between his teeth while his head was strapped into a padded headrest. A small millimeter rule, visible in the photographs, is supported just below his eye in a plane with his pupil. All sequential operations were set in advance through the use of five timers and the operator merely pushed one button to start the apparatus, which ran through its prearranged cycle.

The sizes of the pupil on the completed pictures were measured by projecting the pictures in a film strip projector and enlarging them 20 times, using the small millimeter rule as a standard. The pupils of all *S*s were

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[1] This investigation was supported in part by funds provided for biological and medical research by the State of Washington, Initiative measure No. 171.

measured across the same diameter. The latency was taken as the length of time that elapsed between the onset or cessation of the constricting light and the midpoint between the last picture of the same size and/or direction and the first picture indicating a change in size in the direction determined by the constricting light.

In the first part of the study, *S* was strapped into position in front of the camera and allowed to sit in a completely dark room for 5 min. After this dilation period the camera was started, and pictures were taken for 1 sec. in darkness, followed by 2 sec. of picture taking with the constricting light on, and finally about 9 sec. in darkness again. All pictures were taken at the rate of 20 per second. This sequence gives both contraction and dilation on the same film.

In the second part of the study, the contraction and dilation phases were studied separately. In the contraction phase, pictures at the rate of ten per second were taken for 6 sec. in total darkness, followed by picture taking at the same rate for 6 sec. with the constricting light on. Prior to photographing, *S* had been in darkness for 10 min. In the dilation phase *S* was seated in the apparatus with the constricting light on for 5 min. The camera was started and the light turned off. Pictures were taken at the rate of 20 per second for the first 2 sec.; after this the apparatus automatically switched to a new cycle of taking one or two pictures every 10 sec. for approximately 5 min.

RESULTS

The results of both parts of the experiment are presented in Table 1. This table shows the latencies of the contraction and dilation reactions, the maximum pupil size at the onset of the visible light (after the preliminary reaction to the apparatus, if it occurred), the minimum pupil size attained, the maximum size attained upon redilation, and the percentage of recovery to the original maximum size.

TABLE 1

The Average Contraction and Dilation Latencies, Maximum and Minimum Sizes, and Percentage of Recovery of Part 1 ($N = 10$) and Part 2 ($N = 5$)

MEASURE	CONTRACTION LATENCY (sec.)	DILATION LATENCY (sec.)	MAXIMUM SIZE LIGHT ONSET (mm.)	MINIMUM SIZE (mm.)	MAXIMUM SIZE REDILATION* (mm.)	PER CENT RECOVERY
			Part 1			
Mean	.220	.385	6.66	3.28	6.35	93
SD	.035	.058	.610	.521	.437	
SE$_M$	.012	.019	.203	.174	.155	
			Part 2			
Mean	.175	.180	7.47	3.00	7.18	98
SD	.039	.033	.536	.221	.277	
SE$_M$	.019	.016	.268	.128	.160	

* The maximum size in part 1 at 8 sec.; in part 2, at 5 min.

The pupil sizes at each time interval, $\frac{1}{20}$ sec., were averaged for all ten *S*s of part 1. The mean results were plotted as black dots; the resulting curve for the contraction data appears in Figure 1 and for dilation in Figure 2. These results were empirically fitted with curves of mathematical formulation visible as the continuous lines in Figures 1 and 2. The contraction data are fitted by an equation of the form: $Y - Y_{min} = ke^{-mt}$, where k, m, and Y_{min} are constants, the constant Y_{min} being the minimum pupil diameter in millimeters obtained after prolonged exposure to

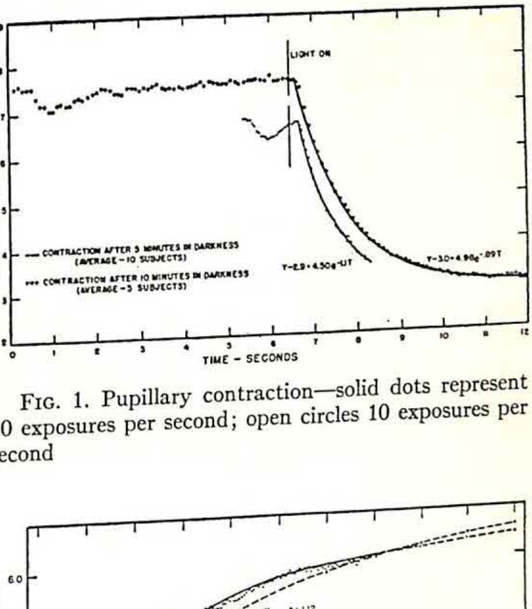

FIG. 1. Pupillary contraction—solid dots represent 20 exposures per second; open circles 10 exposures per second

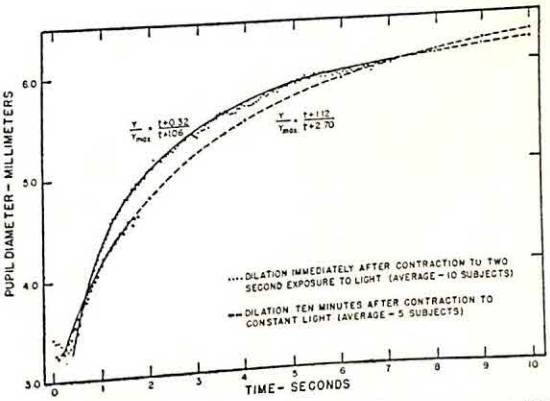

FIG. 2. Pupillary dilation—solid dots represent 20 exposures per second; open circles 20 per second for 2 sec. and one exposure every 10 sec. thereafter. Circles between 2 and 10 sec. are predicted.

the contracting light, Y the pupil diameter at any time after the latent period, and t the time in seconds after the onset of the light. The equation for the contraction data in Figure 1 is $Y - 2.9 = 4.50e^{-1.1t}$, where 2.9 represents an estimated minimum size since the pupil was not allowed to contract to a minimum size. The dilation data of Figure 2, represented by the black dots, were fitted by an equation of the form: $\frac{Y}{Y_{max}} = \frac{t + B}{t + C}$, where B and C are constants, t is time in seconds, and Y_{max} is the maximum pupil size in millimeters reached during dilation. The equation for the dilation data is: $\frac{Y}{6.66} = \frac{t + .32}{t + 1.06}$.

The results of the second part of the study are presented in Figures 1 and 2 as open circles. These data were fitted with equations of the same form as those used to fit the data of the first part of the study. The contraction data were fitted by the equation $Y - 3.0 = 4.98e^{-.89t}$ $.89t$, and the dilation data with the equation $\frac{Y}{7.18} = \frac{t + 1.12}{t + 2.70}$.

If one assumes that there should be no differences between the latency for contraction and the latency for dilation, it is possible to make six comparisons between the various measures. The t test indicates that there is a highly significant difference between the dilation latency of part 1 and each of the other latencies. Differences between any of the other latencies are not significant.

DISCUSSION

The dependence of the results obtained upon the experimental methods used in obtaining them is clearly demonstrated by a comparison of the results of parts 1 and 2 of this study. In part 1, two conditions, the "psychosensory response" (6) and the relatively short exposure of the constricting light (2 sec.) effectively kept the pupil in a state of movement at the onset and the cessation of the light. As the dotted curve in Figure 1 indicates, the pupil was in a process of dilation at the time that the constricting light came on, and it continued to dilate for some time before it started to contract. This continued dilation resulted in a longer latency time than that found in part 2 (circles in Fig. 1), where the pupil had been stabilized before the light came on. A similar conclusion was drawn by Machemer (8), who found that the duration of the contraction latency may be extended to as much as .350 sec. if the constricting light comes on when the pupil is in a dilating phase of its normal unrest. The same influence of a state of activity is even more apparent in the dilation latency, since the dotted curve of Figure 2 shows a continued contraction amounting to .15 mm. before the pupil started to dilate.

The nature of the preliminary contraction and dilation in the contraction curve for part 1 is of interest. The Ss had been seated in a dark room for 5 min. before the camera and infrared lights came on. Though there was no visible light in the room, five of the ten Ss demonstrated a mean contraction of .85 mm., followed by a mean dilation of .57 mm. This total cycle occurred in anywhere from 1 to 4 sec. The mean latency of this reaction was .345 sec. as compared with .215 sec. for the same Ss' reactions to light. There are insufficient data to warrant fitting curves, but the contraction and dilation both appear to be quite similar in shape and steepness of slope to the curves for reaction to light. These similarities do not appear in Figure 1 since the curve there is a composite curve of the five Ss who showed this response and the five who did not. The response appears to be some reaction related to the onset of the camera apparatus. It bears certain resemblances to Lowenstein's "psychosensory restitution phenomenon" (6) in that the reaction is not to the light stimulus but rather to some other environmental stimulus or to an internal stimulus. Lowenstein has been able to restore a pupillary reaction, which had been reduced to nothing by rapid alternation of light and darkness, by threatening S with pain, provided S accepts the threat. He has also found that other emotions, for example joy, and purely sensory stimuli, such as a noise stimulus or the prick of a pin, are capable of bringing about the restoration of the fatigued response. While our situation is different in that S's pupillary response is not fatigued, it is plausible that the reaction to the onset of the apparatus falls in the same category as the "restitution phenomenon." The same response occurs in part 2, but recovery is complete before the constricting light occurs.

A comparison of the two curves in Figure 1 indicates that the curve for contraction after dilation is steeper than the contraction from a stabilized level. This same relationship holds for the dilation curves of Figure 2. No difference was found between the curves of part 1 based on all ten *S*s and on the five *S*s who also served in part 2. No consistent differences were found between male and female *S*s.

When we compare the latencies for dilation found in parts 1 and 2, it appears that the mean latency for reaction to the cessation of light is significantly longer immediately following contraction than following a period of stability. The dilation latency for part 1 is also significantly longer than the contraction latencies found in both parts, while the latency for dilation found in part 2 is not significantly different from either contraction latency, and in fact, is practically identical with the contraction latency of part 2. This near identity strongly suggests that the latencies of reaction are the same for both contraction and dilation and that any differences found are probably due to the amount and type of activity immediately preceding contraction or dilation. The latency values found in either part 1 or part 2 agree quite closely with those found by other investigators who used methods similar to those used in parts of this study. This agreement indicates that the different latencies that have been found may be more a function of technique and conditions than of the pupillary mechanism.

SUMMARY AND CONCLUSIONS

The latencies of pupillary contraction and dilation and the nature of the responses of the pupil to light and darkness were determined under two types of experimental procedure using high-speed photography with infrared illumination. One experimental procedure involved contraction immediately followed by dilation; the second procedure determined one latency at a time after long adaptation to either light or darkness. Ten *S*s varying in age from 21 to 29 were used under the first conditions, and five of the same *S*s were used under the second.

1. When the pupil is in a state of activity, either contracting or dilating (not including the normal fluctuations of the stabilized pupil), both the contraction and dilation latencies are longer than when the pupil is stable immediately before the onset or cessation of light.

2. The mean latency for contraction following activity was found to be .220 sec.; the latency following stability, .175 sec.

3. The mean latency for dilation following activity was .385 sec.; after stability, .180 sec.

4. Under optimum conditions, the dilation latency is approximately equal to the contraction latency.

5. The curves for contraction were fitted with the following equations:
Following activity: $Y - 2.90 = 4.50e^{-1.1t}$,
Following stability: $Y - 3.00 = 4.98e^{-89.t}$,
where Y equals pupil size in millimeters and t is time in seconds.

6. The curves for dilation were fitted with the following equations:

$$\text{Following activity: } \frac{Y}{6.66} = \frac{t + .32}{t + 1.06},$$

$$\text{Following stability: } \frac{Y}{7.18} = \frac{t + 1.12}{t + 2.70},$$

where Y is pupil diameter in millimeters, Y_{max} is the maximum diameter in millimeters, and t is time in seconds.

7. Five *S*s showed a definite reaction (consisting of a contraction and immediate redilation) to the onset of the apparatus while still in the dark. The mean latency of their reactions was .345 sec., in contrast to their mean latency of reaction to light of .215 sec. The mean contraction was .85 mm. and the mean redilation was .57 mm.

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Received September 21, 1953.

CORTICAL CORRELATES OF AUDITORY LOCALIZATION AND OF RELATED PERCEPTUAL PHENOMENA[1]

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Much is known about the dependence of auditory localization on stimulus conditions, but little is known about the neural processes involved in localization. By the beginning of the nineteenth century it was recognized that localization of sounds generally depends upon differences between the stimulus conditions at the two ears. Among the first to control the interaural differences by stimulating the two ears independently was Alison (2). He interpreted his results as consistent with the hypothesis, already current, that localization depends upon differences in the *intensity* of the stimuli at the two ears. This intensity-difference hypothesis was established firmly by Lord Rayleigh in 1876–77 (16, 17). Rayleigh mentioned the possibility that localization might also depend upon differences in time of arrival of stimuli at the two ears, but he rejected this hypothesis. The time-difference hypothesis appears to have been first proposed seriously by Mallock in 1908 (11) and to have been first demonstrated experimentally by Aggazzotti in 1911 (1). During the first world war, French (14) and German (8) scientists who worked on sound locators confirmed and elaborated the time-difference hypothesis. Since that time, many psychophysical studies have helped to define the functional dependence of localization upon interaural differences of time and intensity (15, 21).

Several investigators have proposed hypothetical neural mechanisms to account for auditory localization. According to most of these hypotheses, differences in the perceived localization of a sound are determined by differences in the place of activity in the nervous system. Perhaps the first "place hypothesis" is that of Bowlker, who proposed in 1903 "that the point where the impulses [from the two ears] meet is the focus that gives rise to the sensation of the sound image" (5, p. 327). More or less elaborate place hypotheses have been proposed by Piéron (14, 15), Boring (4), Békésy (3), and Jeffress (9). Apparently none of these hypothetical mechanisms has been tested experimentally.

Recently the electrical activity of the brain has been studied in order to gain information about the neural processes involved in auditory localization. Using this approach, Tunturi (23) has demonstrated interaction of impulses from the two ears at the medial geniculate body and at the auditory cortex. That is, the response to stimulation of both ears together was not a simple summation of the responses to separate stimulation of the two ears. In previous papers we have described some characteristics of cortical responses to single auditory click stimuli (18) and to paired clicks (19). In this paper we will examine cortical responses for information about cortical correlates of auditory localization and of related perceptual phenomena.

METHOD

Electrophysiological responses were recorded at the auditory cortex of anesthetized cats. The stimulus conditions of psychophysical experiments on auditory localization were duplicated by stimulating the two ears independently; clicks were delivered from separate earphones, one earphone coupled to each ear. The intensities of the clicks and the time differences between paired clicks were varied. The electrophysiological responses were recorded photographically from the face

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[1] This article is based in part upon a doctoral thesis presented to the Faculty of Arts and Sciences, Harvard University, and in part upon further research. An earlier report, "Neural Correlates of Auditory Localization," was read at the Eastern Psychological Association, April 8, 1949. I wish to thank Dr. R. Galambos for introducing me to many of the physiological procedures employed in this study. He and Drs. E. B. Newman and W. A. Rosenblith gave helpful counsel throughout the course of the research. Professors E. E. Ghiselli and D. Krech of the University of California read the manuscript and made many helpful suggestions.

This research was carried out under Contract N5ori-76 between Harvard University and the Office of Naval Research, U.S. Navy (Project NR 142-201). Reproduction for any purpose of the U.S. Government is permitted.

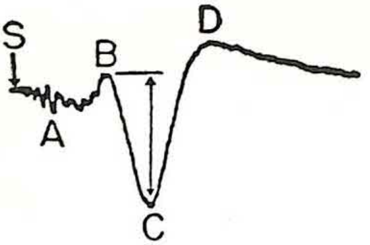

FIG. 1. Electrical response of area I of the auditory cortex. The response was evoked by stimulating one ear with a brief click.

of a cathode-ray oscilloscope. The methods have been described in detail previously (18, 19).

It will be convenient to refer to the first of a pair of stimuli as $S1$ and to the second member of the pair as $S2$. The corresponding cortical responses will be called $R1$ and $R2$. The time interval between $S1$ and $S2$ will be called the delta interval.

RESULTS

The Cortical Response to a Single Click

Figure 1 shows a response recorded at area I of the auditory cortex when a click stimulus was delivered to one ear. The delivery of the stimulus is marked by the arrow, *S*, at the start of the trace. After a latency of a few milliseconds, small wavelets like those at *A* often appear at the cortex. These represent the electrical spread to the cortex of responses originating at subcortical centers of the auditory system. Next, there is often a negative deflection like the one at *B*. (A negative potential produces an upward deflection in our recording system.) The peak of this deflection usually has a latency of 6 to 10 msec. The negative deflection does not appear at every location in the auditory area. The most characteristic component of the cortical response is the large positive deflection shown at *C*. The latency of its peak varies from 8 to 15 msec., depending upon the location of the electrode within the auditory area and upon the intensity of the stimulus. The amplitude, measured as indicated by the arrow in the figure, may vary from only a few microvolts to a few hundred microvolts; the amplitude also depends upon electrode location and upon stimulus intensity. Finally, the positive deflection is often followed by a negative deflection like the one at *D*. The positive deflection has been attributed to the activity of cortical interneurons and the final negative deflection to the corticofugal discharge of large pyramidal cells (6). When one ear is stimulated, responses can be recorded throughout the auditory areas of both cerebral hemispheres. However, the responses are significantly larger in amplitude at the hemisphere contralateral to the ear that is stimulated. In a survey of 49 electrode locations in five cats, the contralateral response was significantly larger than the ipsilateral response at 28 locations. Neither response was significantly larger at 20 of the locations. The ipsilateral response was significantly larger at only one of the 49 locations (18).

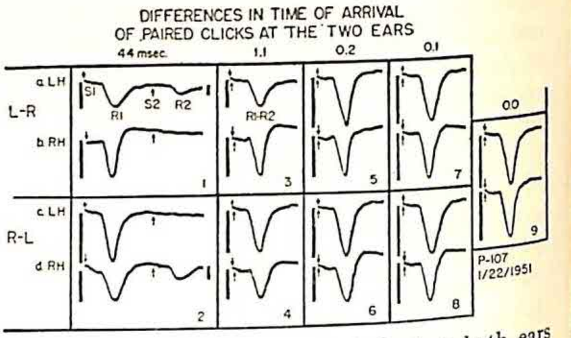

FIG. 2. Cortical responses evoked when both ears were stimulated with clicks. The two responses in each block were recorded simultaneously at the two hemispheres. The upper response in each block was recorded at the left hemisphere (LH) and the lower response in each block at the right hemisphere (RH). The stimulus conditions are described in the text.

Cortical Responses to Pairs of Stimuli

Figure 2 shows responses obtained from animal P-107 when both ears were stimulated. The two responses in each block of the figure were recorded simultaneously from the two cerebral hemispheres. The upper trace in each block was recorded at the left hemisphere (LH); the lower trace in each block was recorded at the right hemisphere (RH). The upper row of blocks was recorded when the first stimulus was delivered to the left ear and the second stimulus to the right ear (L-R); in the lower row, $S1$ went to the right ear and $S2$ to the left ear (R-L). The stimuli to the two ears were kept equal in intensity throughout the experiment. The delivery of $S1$ is indicated by an arrow above the start of each trace; the delivery of $S2$, by an arrow below the trace. The distance between the $S1$ arrow and the $S2$ arrow indicates the delta interval. In this figure the subcortical wavelets are very small and only the positive deflection is prominent. Fifteen pairs of responses were recorded under each stimulus condition in this experiment; the pairs shown in the figure were those closest to the mean for each condition.

In blocks 1 and 2, *S*1 preceded *S*2 by 44 msec. With this delta interval, the first response (*R*1) was complete by the time *S*2 was delivered. At each hemisphere, the response is larger when the contralateral ear is stimulated than when the ipsilateral ear is stimulated. When *S*1 was delivered to the left ear, *R*1 was larger at RH (line *b*) than at LH (*a*). (To facilitate comparison, the amplitude of each response is shown by the height of the bar placed beside the response. The amplitude measures will be presented graphically in Fig. 3.) When *S*1 was delivered to the right ear, *R*1 was larger at LH (*c*) than at RH (*d*). Sometimes, as with this animal, the latency of the response to contralateral stimulation is less than the latency of the ipsilateral response, but this is not always the case.

Before leaving blocks 1 and 2, note that *R*2, the response to *S*2, appears only in lines *a* and *d*; *R*2 does not appear in lines *b* and *c*. The reasons for the failure of *R*2 to appear in *b* and *c* will be discussed later in connection with Figures 4 and 5.

In blocks 3 through 9, where the delta interval is 1 msec. or less, *R*1 and *R*2 fuse into a single response (*R*1–*R*2). The fused responses tend to be larger when *S*1 goes to the contralateral ear and *S*2 to the ipsilateral ear (lines *b* and *c*); the responses tend to be smaller when the ipsilateral ear is stimulated first and the contralateral ear second (*a* and *d*). The fused responses are maximum when the stimuli to the two ears are simultaneous, as in block 9.

The electrode locations on the two hemispheres were closely similar in this experiment. Nevertheless, the responses recorded at the two locations were not absolutely symmetrical. Therefore, the most critical comparisons can be made among the responses at a single electrode location rather than between the responses of the two locations. For the LH location, we can compare the responses of lines *a* and *c*. At the delta interval of 1.1 msec., the L-R response (*a*) is much smaller than the R-L response (*c*). But at 0.2 and 0.1 msec., the L-R and R-L responses are about equal. At the RH location, the L-R responses (*b*) remain larger than the corresponding R-L responses (*d*) throughout the series—even at delta intervals of 0.2 and 0.1 msec.

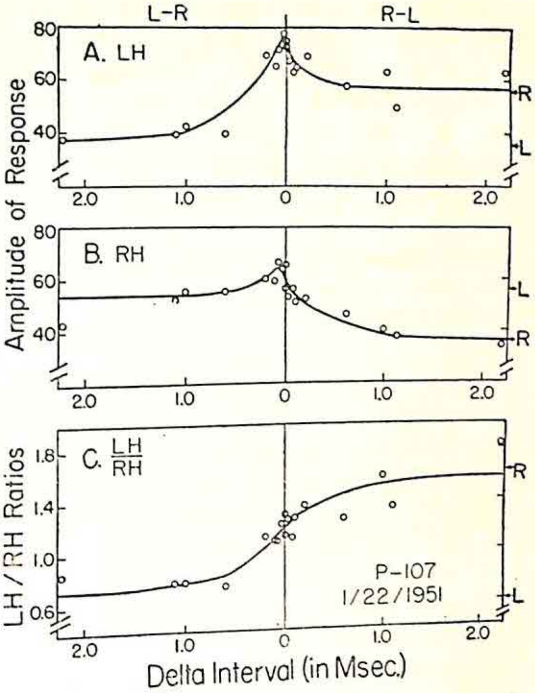

FIG. 3. *A*. Mean response amplitude versus delta interval (in msec.). The responses were recorded at the auditory area of the left cerebral hemisphere. *B*. Mean response amplitude versus delta interval. Responses recorded at right hemisphere. *C*. Ratio of left hemisphere response to right hemisphere response versus delta interval.

The variation of response amplitude with stimulus conditions can be seen more precisely and for a larger number of delta intervals in the graphs of Figure 3. Each point in these graphs represents the mean of 15 responses recorded under one stimulus condition. Graph *A* presents the function of response amplitude versus delta interval for the LH location. The function rises to a peak in the center around a delta interval of zero. As the delta interval is increased from zero, the function falls off more rapidly on the L-R side than on the R-L side. By about 0.3 msec., the L-R response is clearly smaller than the corresponding R-L response. About 1 msec. out from the center on both sides, relatively flat plateaus begin. The amplitude of the responses on the L-R plateau is only about two-thirds the amplitude of the responses on the R-L plateau.

Responses to stimulation of each ear alone were also recorded; their amplitudes are indicated by the L and the R in the right margin of the graph. It can be seen that on the L-R side, the function becomes asymptotic to the amplitude of the L response. On the R-L side, the function becomes asymptotic to the R response. In other words, stimulating with L-R approximates stimulating with L alone, the more so the larger the delta interval. Similarly, stimulating with R-L approximates stimulating with R alone.

At the RH location, in graph *B*, the function is almost the mirror image of the LH function. Here the L-R plateau is about one and one-half times as high as the R-L plateau. Even at the center peak, the L-R responses are larger than the corresponding R-L responses at all delta intervals. As in graph *A*, stimulating with L-R approximates stimulating with L alone, and stimulating with R-L approximates stimulating with R alone. Both the RH and the LH functions are slightly off center to the left.

The data from the two hemispheres can be combined into a single function by plotting the ratio of the LH response to the RH response for each stimulus condition. Graph *C* of Figure 3 presents these LH/RH ratios. When the left ear alone is stimulated, there is less activity at LH than at RH; in this experiment, the LH/RH ratio for stimulation of the left ear was about 0.6. When the right ear was stimulated, the ratio was about 1.6. Graph *C* covers almost the whole range between the L and R conditions, and it shows a continuous transition from one to the other as the delta interval is varied. At the extreme left of the graph, with an L-R interval of 2.2 msec., the ratio is almost as low as when the left ear alone was stimulated. Following the curve from the left toward the right, we see the ratio rise gradually as the delta interval decreases. Then, at an interval of about half a millisecond on the L-R side, the curve begins to rise more rapidly. The steeper slope persists until the curve reaches a delta interval of about half a millisecond on the R-L side. Then the rise becomes gradual again. At the extreme right, the ratio approximates the value obtained when the right ear alone was stimulated. Thus, the ratio of activity at the two hemispheres can be varied from the L value to the R value by using appropriate L-R and R-L stimulation.

Although most of our experiments have dealt only with time differences, some have also set intensity differences against time differences. If the intensity of $S1$ is attenuated sufficiently while the intensity of $S2$ is held constant, the ratio of activity at the two hemispheres can be inverted. With an appropriate change in the *intensities* of the stimuli, the fused response is altered as if the *temporal order* of the stimuli had been reversed. The greater the delta interval, the greater the intensity difference that is needed to overcome it. Observations from two experiments indicate that an intensity difference of 10 db can balance out a time difference of the order of 0.1 msec.

The Response to the Second Stimulus

The amplitude of $R2$ also changes systematically as a function of the delta interval. But whereas $R1$ is affected only when the delta interval is less than about 10 msec., $R2$ may be affected when it follows $R1$ by as much as a second. Figure 4 shows the functions of both $R1$ and $R2$ for delta intervals up to 150 msec. The solid lines show $R1$ and, at the smaller delta intervals, the fused $R1$–$R2$ response. These curves reveal similar characteristics to those we saw in graphs *A* and *B* of Figure 3.

Now let us examine the $R2$ functions (the broken lines). These functions are considerably depressed in amplitude at the smaller delta intervals. As we follow the $R2$ functions toward larger delta intervals, we see $R2$ recover its amplitude. The recovery goes through a maximum at around 100 msec. and then declines again. It is clear that the $R2$ function is lower on the R-L side at LH and on the L-R side at RH. There are two reasons for this asymmetry: (*a*) In both cases, $S2$ goes to the ipsilateral ear, which generally elicits a smaller response. (*b*) The depression of $R2$ is proportional to the amplitude of $R1$. Where $S1$ goes to the contralateral ear, $R1$ is larger and $R2$ is consequently further depressed. We saw a similar occurrence in Figure 2, blocks 1 and 2, where $R2$ did not appear in lines *b* and *c*; there also, $S1$ went to the contralateral ear and $S2$ to the ipsilateral ear.

When the $R2$ curve is extended to longer

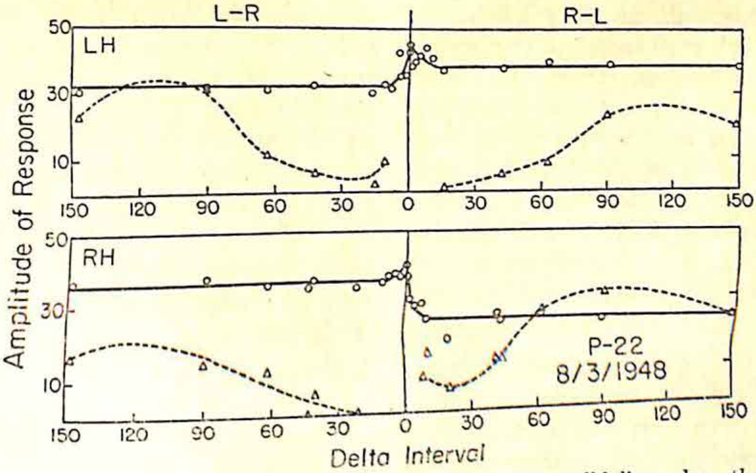

FIG. 4. Mean response amplitude versus delta interval (in msec.). The solid lines show the amplitude of the first response ($R1$); the dotted lines show the amplitude of the second response ($R2$).

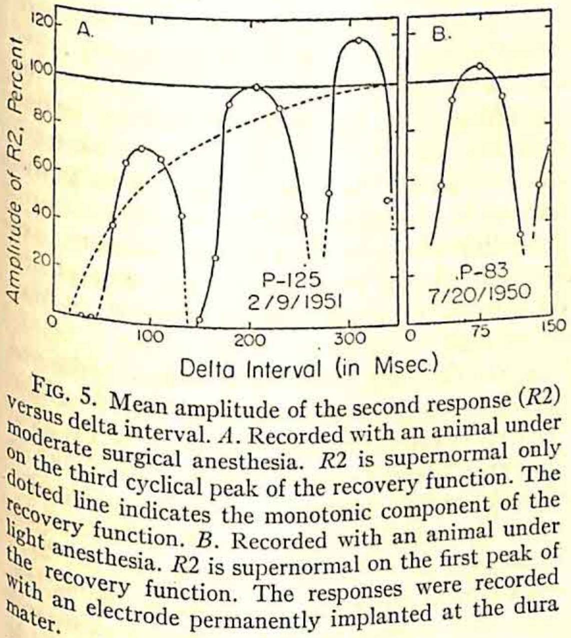

FIG. 5. Mean amplitude of the second response ($R2$) versus delta interval. *A*. Recorded with an animal under moderate surgical anesthesia. $R2$ is supernormal only on the third cyclical peak of the recovery function. The dotted line indicates the monotonic component of the recovery function. *B*. Recorded with an animal under light anesthesia. $R2$ is supernormal on the first peak of the recovery function. The responses were recorded with an electrode permanently implanted at the dura mater.

delta intervals, it shows a generally rising trend upon which cyclical variations are imposed (19). In some cases $R2$ becomes supernormal at some of the cyclical peaks of the recovery function, as in Figure 5. In particular, this supernormality may occur on the first peak of the recovery function if the anesthesia is sufficiently light. Figure 5*B* shows a case in which the first peak of the recovery function was supernormal between delta intervals of about 60 and 90 msec.

DISCUSSION

In order to consider whether these cortical events run parallel to perceptual phenomena, it will be necessary to review briefly the perception of paired clicks. As each aspect of the perceptual phenomena is mentioned, an attempt will be made to point out correlated cortical events. I do not mean to imply that the processes underlying the perceptual phenomena are necessarily cortical. Impulses from the two ears are known to interact at least as low in the afferent system as the inferior colliculus (20). I wish only to demonstrate correlations between the cortical events and the perceptual phenomena. In most cases I will not try to suggest the mechanisms of the observed cortical events; the mechanisms of these events will be considered separately elsewhere.

In attempting to correlate the cortical data with the available psychophysical data, I shall assume that the cat localizes sound much as the human does. It would not be necessary to make this assumption if we could obtain both cortical records and perceptual data from a single species. But, at present, cortical records can best be obtained from animals (surgical intervention being necessary in order to record the primary responses of the human auditory area). And psychophysical judgments can best be obtained from human observers, although some measurements of localization have been made in the cat (10, 12).

Considering only interaural time differences, we may assume that the cat localizes less precisely than man. The cat's ears are only about one-third as far apart as man's ears; therefore the cat receives interaural time differences that are only about one-third as great as those which man receives. It may be objected that tests have not shown the cat to localize more poorly than man, and the bat, with a much smaller head size, localizes well. But under natural free-field listening conditions, we cannot consider only time differences; there are also differences of intensity between the two ears. These interaural intensity differences are greater the higher the frequency of the sound. The smaller the size of the head (or, more properly, of the cochlea), the higher the frequency an animal can hear. Thus, the ability of animals with small heads to hear high frequencies may compensate, in localization, for the small interaural time differences that are available to them.

Now let us note what an observer reports when his ears are stimulated by single or paired clicks presented by earphones. And let us note the cortical correlates:

1. If only one ear is stimulated, the observer can report without error which ear it is. A previous analysis (18) has indicated that each ear is represented by a larger population of cortical units at the contralateral cerebral hemisphere than at the ipsilateral hemisphere. Therefore, when one ear alone is stimulated, the cortical responses are larger at the contralateral hemisphere. We have seen this in Figures 2, 3, and 4.

2. Now let us stimulate both ears of our observer. We will start with the clicks simultaneous, and then we will introduce delta intervals between the clicks. When his ears are stimulated simultaneously (and with clicks of equal intensity), the observer usually hears the sound in the median plane. With this stimulus condition, the cortical activity is usually equal at the two hemispheres. Some observers hear the sound slightly off to one side when the clicks at the two ears are simultaneous (24). To have the sound centered, such observers require the introduction of a small delta interval or a small difference of intensity favoring the opposite direction. The animal of Figure 3 may have had a slight bias of this sort to the right, for the peaks of the curves seem to fall just to the left of zero.

3. When *S*1 precedes *S*2 by about 30 msec., an acute observer begins to hear the sound very slightly off center toward the side of *S*1 (15, 21). In most cases we have not tried to determine the threshold delta interval at which L-R or R-L responses first differ significantly from responses to simultaneous stimuli. In several cases, however, we have found a significant difference at 100 msec. and, in some cases, at 50 msec. At this threshold, the cortical responses reveal which ear is stimulated first. At each hemisphere the fused response resembles a response to *S*1 more than it resembles a response to *S*2. As we saw in Figure 3, the L-R response approaches the response to L alone, and the R-L response approaches the response to R alone. When the ratio of the responses at the two hemispheres is taken, a relatively low LH/RH ratio indicates L-R stimulation; a relatively high ratio indicates R-L stimulation.

4. If the intensity of *S*1 is attenuated sufficiently, the observer hears the sound move back to the median plane or even cross it to the other side. This has been reported by several experimenters (3, 15, 21), though they have not agreed closely on how much intensity difference is needed to balance out the effects of time differences. In the cortical responses, too, we have found that the effects of intensity differences could balance out the effects of time differences.

5. As the delta interval is increased, the observer hears the sound move further from the median plane and toward the interaural axis. The displacement from the median plane is directly proportional to the delta interval until the sound reaches about 10° from the interaural axis. Then the course along which the sound is moving shows a bend. Thereafter, the sound approaches the interaural axis more slowly. The delta interval at which this bend is reached has been reported as 0.63 msec. (8), 1.44 msec. (22), and 0.45 msec. (3). Figure 2 shows some correlation with the description of these perceptual changes. If we go from the center of any of the functions toward the plateau on either side, most of the change occurs rapidly before the 0.5-msec. point is reached. Beyond this point the functions continue to change, but the changes proceed more slowly. In some animals the transition from the L-R plateau to the R-L plateau occurs more slowly; this is the case in Figure 4. There the curves take 3 or 4 msec. to drop halfway from the center peaks to the plateau. But with most animals, most of the main

transition occurs rapidly within delta intervals of 1 msec. or less.

6. The observer continues to perceive a single sound at the side of *S*1 until the delta interval reaches about 2 or 2.5 msec. (24); then he hears a faint click at the side of *S*2 as well as the strong click at the side of *S*1. It is interesting that fusion persists until 2 msec. separate *S*1 and *S*2, for this is more than twice as long as the maximum delta interval that can occur in nonlaboratory situations. If the two ears are not isolated artificially and if a sound is produced at one ear, the sound takes only about 0.8 msec. to travel around the head to the other ear. In the cortical records it is often possible to see a second response starting before the first response is over. *R*2 rides on the tail of *R*1. Since the responses overlap, they are hard to measure. Moreover, the use of anesthesia makes *R*2 recover its amplitude more slowly than normally. It is difficult to determine the exact interval at which fusion of *R*1 and *R*2 breaks down, but it is clearly under 10 msec.

7. As the delta interval increases beyond 2.5 msec., the observer hears the click at the side of *S*2 increase in loudness. At about 10 msec., it becomes louder than the click at the side of *S*1. This enhancement of the second click continues past an interval of 100 msec. (7). Because the anesthesia affects the recovery cycle of *R*2 in the experimental animals, no very close correlate to normal perception can be expected. But under light anesthesia, *R*2 may become supernormal on the first peak of the recovery function. In one case, supernormality of *R*2 was observed between delta intervals of about 60 and 90 msec.

8. A somewhat different type of correlate can be sought if we can open an observer's skull and stimulate his brain electrically. Penfield and his collaborators have stimulated the auditory area directly in conscious observers (13). When stimulation occurs, the observer reports hearing sounds. With stimulation of different points on one hemisphere, the observer hears sounds in either of two locations. He reports that most sounds are contralateral to the stimulated hemisphere; some sounds are heard "bilaterally"; no sounds are heard ipsilaterally. At the cat's cortex, it will be remembered that the contralateral response was significantly larger than the ipsilateral response at most locations; presumably these are similar to the points which, when stimulated electrically, give rise to a contralateral sound. These are also the points at which localization effects can be observed most readily. There were also locations at which neither response was significantly larger; presumably these, if stimulated, would give rise to "bilateral" sounds. Only one location was found at which the ipsilateral response was significantly larger.

SUMMARY

Electrophysiological responses were recorded at the auditory cortex of anesthetized cats. The stimulus conditions duplicated those of psychophysical experiments on auditory localization. The two ears were stimulated independently with clicks. Differences in the time of arrival of clicks at the two ears and differences in intensity of the clicks were varied. The dependence of cortical responses on these stimulus conditions was determined. The cortical events were found to parallel in several respects the perceptual phenomena which occur under the same stimulus conditions.

Among the cortical correlates of auditory localization are the following:

1. Under the stimulus conditions that cause a sound to be heard at one side of the head, the cortical activity is greater at the contralateral cerebral hemisphere.

2. The further over to the side the sound is heard, the greater the difference between the activity at the two hemispheres.

3. When the sound is heard in the median plane, the cortical activity is equal at the two hemispheres.

Cortical correlates were also found for two related perceptual phenomena—perceptual fusion of closely successive sounds and enhanced loudness of the second of two clicks.

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Received October 15, 1953.

THE EFFECTS OF FRONTAL LOBE DAMAGE UPON HABIT REVERSAL IN THE WHITE RAT

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In order to understand the functions of the brain, a prior task is to find measures of performance which are sensitive to brain damage. The present experiment concerned itself with that task, by investigating the general hypothesis that rats with frontal lobe lesions are less able to learn to reverse certain learned problems than normal animals.

Relatively few studies have investigated the behavior of brain-damaged lower animals on tasks of reversal learning per se. Stereotyped behavior of the organism after cortical injury has been noted, with emphasis upon the difficulty that operated animals have to learn new habits and break old ones. Tolman (18) noted that normal rats show more "vicarious trial-and-error" than operated animals; Hamilton and Ellis (6) found an increase in "behavior constancy" in operated rats; Settlage *et al.* (17) spoke of "perseverative interference" in prefrontal monkeys; and Krechevsky (10) reported lessened "fluidity of hypotheses" of operated rats.

A large part of the work relating to habit reversal has been done by Harlow and his co-workers (7). The results of this significant group of studies cannot be summarized here beyond noting that they point toward reversal problems as showing the greatest deficit in operated animals.

The above terms are reminiscent of those used to describe characteristics of brain-damaged human *S*s: inability to shift from one type of experience to another, perseveration, inability to divide attention, impairment in the ability to abstract (5). The point may be argued that these are analogous phenomena.

PROBLEM

Lashley (13) originally felt that the more complex the maze problem to be learned, the greater the retardation produced by any given extent of lesion. Although later experimentation (15) led Lashley to conclude that the relative difficulty of the simple and complex mazes was the same for operated and control animals, the effect of increasing complexity upon reversal learning was not investigated. In contrast, Erickson (2), Jacobson (8), and Warden, Barrera, and Galt (19) have pointed out that learning complex problems is more adversely affected by cerebral damage than learning simple problems. These studies were also not concerned with reversal learning.

This background of experiments leads to the expectations, relevant to the present study, that operated rats cannot learn to reverse a simple maze problem as readily as controls and, compared with control animals, operated rats will show increased perseverative interference as the difficulty of the task is increased.

Lashley (12) found that even after complete destruction of the area striata, habits based on brightness discrimination were abolished, but could be reformed at exactly the same rate as the original formation in normal animals. If frontal lesions affect the ability of rats to learn brightness discrimination *reversal*, this would suggest that the ability to learn reversal of brightness discrimination is a function different from that of learning brightness discrimination itself, a function which is more "sensitive" to brain lesions than original learning.

Conversely, reversal ability may not be a discrete and independent ability which is always affected by frontal damage. Perhaps the ability to learn the reversal of a given problem depends upon the nature of the given problem and the demands it makes on the frontal cortex. If the original learning does not depend upon the frontal lobe, as is the case in brightness discrimination, perhaps the ability

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[1] Now at the New Orleans Regional Office, Veterans Administration. For more detailed information the reader is referred to the dissertation presented to the faculty of the Department of Psychology of Tulane University from which this article is taken. The author expresses his appreciation to Dr. Loh Seng Tsai, chairman of the dissertation committee, and to other members of the committee.

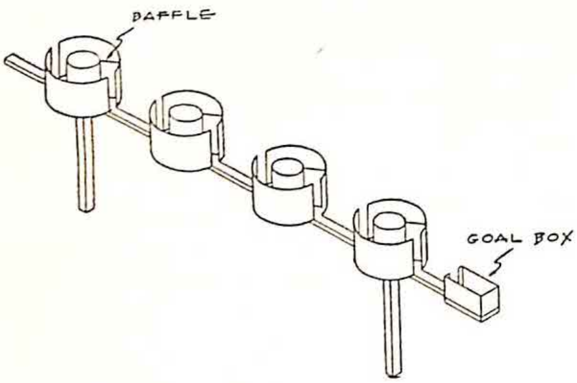

FIG. 1. Maze apparatus

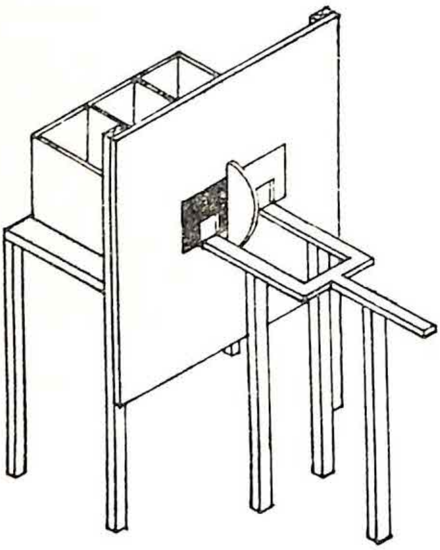

FIG. 2. Discrimination apparatus

to learn the reversal of this problem also does not depend upon the frontal lobe.

Gatling (4) found that negative transfer effect is eliminated in a series of stimulus reversal problems. Normal rats show evidence of "learning to learn" in successive reversals. Do the results found with normal rats also obtain with rats with frontal lesions, or does the successive reversal produce perseverative interference and thus constitute a progressively harder task for operated *S*s as compared with controls?

METHOD

Apparatus

The unidirectional maze (Fig. 1) used in the experiment consisted of four round maze units, 1 ft. in diameter, mounted at intervals of 16 in. on an elevated linear pathway. The apparatus could be used as a single unit or as a four-unit maze. Plastic doors, hinged above the exit of each unit, prevented retracing between units. Reliability of the maze apparatus, computed from errors made by control animals, was determined from a correlation of odd versus even trials, corrected by the Spearman-Brown formula. The four-unit maze yielded a reliability coefficient of .89.

The reliability of the discrimination apparatus (Fig. 2), modeled after the Lashley Jumping Box, was computed from errors of control animals on original learning. A correlation of odd versus even trials, corrected by the Spearman-Brown formula, resulted in a reliability coefficient of .84.

The thermocautery used to produce the brain lesions was similar to those obtainable from any medical supply house. A foot switch controlled the current, which was drawn from a variable transformer set at 5 v. Voltage input was 115 v. The cautery drew 5 amp. of current.

Subjects

Sixty experimentally naive albino rats were divided into two main groups, 30 which learned the maze problems and 30 which learned the discrimination problems. One-half of each group was operated upon; one-half served as controls, undergoing a sham operation. Split-litter technique was used. The two groups were matched for sex.

Procedure

Operative procedure. Brain operations were performed under deep ether anesthesia. Under aseptic conditions, a mid-line scalp incision about 3 cm. long was made, exposing the frontal sutures of the skull. The cautery was applied ½ cm. anteriorly to the frontal suture, on both sides of the sagittal suture. This method of producing brain lesions by electrocautery without opening the skull was described by Dennis and Bolton (1).

The cautery was applied for a period of from 35 to 40 sec. The scalp flaps were then joined and fastened with metal wound clips. Wound clips were removed on the seventh postoperative day, under a light ether anesthesia.

Control animals were subjected to a sham operation to equalize some of the effects of operative shock. The procedure used was the same as that for the operated group, except that the electrocautery was not applied. Fourteen days were allowed for recovery from operative shock.

Upon completion of the tasks that comprised either problem, histological studies were made of the brains of all operated animals. The brains were frozen, sectioned at 50 millimicrons, and stained with Weil stain by a technician of the Tulane University physiology department. The method of reconstructing the brain diagrams is the same as that used by Lashley (13). The percentage of the total surface area destroyed, as determined from reconstructed diagrams, ranged from 1 to 6.

Training. Preliminary training on the maze consisted in placing each animal at the entrance of the round unit near the goal box and allowing it to explore the unobstructed maze and obtain food. Each animal was given five trials on each of the ten days set aside for habituation. For reinforcement, each animal received five pellets of canned dog food, which amounted to approximately 2 gm. They were then returned to the home cage and fed for 1 hr.

Following the ten-day period of preliminary training, performance on the simple maze problem was begun. One of the two paths leading to the goal was blocked. The task for the rat was to learn to choose the one pathway leading to the goal which was not obstructed. The position of the obstruction was varied so that it blocked the left path for the first five operated and the first five control animals. For the second ten animals the obstruction was placed in the right pathway, and for the third it was placed on the left.

Five massed trials a day were given each animal; retracing to the correct pathway was permitted. Reinforcement was given as during the preliminary training period, and after five trials, the animals were returned to their home cages and fed. Water was constantly available.

After the *S* had learned the problem to the criterion of 96 per cent correct, i.e., one error in 25 trials, the position of the obstruction was changed and the animal started on Task II, the reversal problem, the following day. The task for the rat was to learn to choose the previously blocked pathway, which was now unobstructed. The path that *S* had formerly learned to use was blocked.

After learning the reversal of the simple maze to the criterion, the animal was started on the complex problem, Task III, the following day. The four-unit maze differed from the simple maze only in that three additional maze units had to be learned. The task for the rat was again to learn to choose the pathway that had previously been obstructed. All four units were blocked on the same side. The criterion remained one error in 25 trials. The criterion is actually more difficult on the complex problem, since each trial contained the possibility of making an error in each of the four units. One error in 25 trials therefore means that 99 correct choices had to be made out of 100. When this criterion was reached, the position of the obstruction was again reversed, and *S* started on the new task, Task IV, the following day.

An error was defined as the animal's entry into an incorrect alley beyond one-half the body length. Behavior notes, errors, and the number of trials necessary to reach the criterion were recorded. Both simple and compound errors were counted. A simple error is an uncomplicated error, counted when the rat went to the blind alley, retraced its path, and then made the correct choice. Compound errors were counted when the rat made repetitive incorrect choices in the same unit.

Preliminary training on the discrimination problem was also begun 14 days after operation. Similarly, five trials a day were given, during which *S*s were reinforced with about 2 gm. of canned food. A systematic forced equalization of choice in pretraining was used to reduce color and position preferences, since the animal either freely chose all combinations of color and position or they were forced upon him. Each animal had the experience of being rewarded in the black goal box and the white goal box, as well as being rewarded on the left and on the right side.

After running five massed trials as described, the animal was returned to the home cage and allowed to eat for 1 hr.

Discrimination learning proper, Task I, was begun after ten days of preliminary training. The specific task for *S* was to learn which of the two stimuli, black or white, was being rewarded, and to choose that stimulus regardless of its position.

Black was made the initial correct stimulus for seven control and seven operated rats. For the remaining eight controls and eight operated animals, white was made the initial correct stimulus. This distribution of white to black favors the operated animals slightly. Krechevsky (11) has shown that normal animals have a preference for black alleys, while cortically operated animals prefer white alleys. The above proportions were chosen so that any obtained deficit in learning could not be ascribed to color-preference differences between operated and control animals.

Five massed noncorrection trials a day were given, the position of the rewarded stimulus following a predetermined order. When the animal entered the correct goal box, a small pellet of canned dog food was dropped into a glass food dish. Five such pellets totaled about 2 gm. After running five trials, the animal was returned to the home cage and fed.

Not more than one error for each block of five trials for three days was allowed. When this criterion of 80 per cent correct was reached, the rewarded stimulus was reversed and Task II begun. After learning to respond to the new correct stimulus, the previously unrewarded one, the stimulus was again reversed and Task III begun.

RESULTS

Maze

The test for determining the significances between means of samples drawn from positively skewed populations, devised by Festinger (3), was applied.

The data appear to support these conclusions:

1. There was no significant difference between operated and control rats in ability to learn a simple maze problem. The difference between the two samples was not significant at the .05 level when compared for mean number of trials to criterion, mean number of simple errors, or mean number of compound errors.

2. There was a significant difference between the two samples in ability to learn reversal of a simple maze problem. When errors are compared, either compound or simple errors, the differences between the two groups are significant at the .02 level. When trials are compared, the differences are significant at the .05 level.

TABLE 1
Maze Problem: Group Differences

TASK	OPERATED *S*s	CONTROL *S*s	*F*	*p*
A. Mean Number of Trials				
I	78.13	76.07	1.03	>5
II	63.07	43.00	1.47	<5
III	70.47	83.53	1.18	>5
IV	85.87	46.47	1.85	<2
B. Mean Compound Errors				
I	32.87	19.47	1.69	>5
II	25.00	8.20	3.05	<2
III	69.80	20.53	3.39	<2
IV	82.00	15.73	5.21	<2
C. Mean Simple Errors				
I	31.60	18.00	1.75	>5
II	23.07	7.53	3.06	<2
III	59.80	18.80	3.18	<2
IV	75.33	15.00	5.02	<2

TABLE 2
Discrimination Problem: Group Differences

TASK	OPERATED *S*s	CONTROL *S*s	*F*	*p*
A. Mean Errors				
I	59.0	40.4	1.46	>5
II	142.1	101.5	1.40	>5
III	61.0	70.8	1.16	>5
B. Mean Trials				
I	136.0	100.3	1.36	>5
II	250.9	194.3	1.29	>5
III	117.7	135.7	1.15	>5

3. It must be recognized that the same 30 animals were used in all maze problems. It is methodologically unsound to say without qualification that the larger differences between the two groups on Task IV, compared with the smaller differences between them on Task II, are due to the complexity of the problem alone. Perseverative interference, the influence of learning the first problem upon subsequent problems, is involved. It may be concluded that compared with controls, operated animals show increased perseverative interference as the difficulty of the problem is increased. On the complex problem reversal, the differences between the two groups were significant at the .02 level when compared for trials. The differences in mean trials for the simple reversal were significant at the .05 level only.

Discrimination

As with the maze data, Festinger's test was used to evaluate the significance of the differences in the means obtained from operated and control *S*s.

Under the conditions of the experiment, the following conclusions appear to be justified by the results:

4. There was no significant difference between operated and control rats in ability to learn the original brightness discrimination problem. The obtained differences between the two groups were not significant at the .05 level when compared for mean number of trials to criterion and when compared for mean number of errors.

5. There was no significant difference in the ability of the two samples to learn the reversal of the brightness discrimination problem. Comparisons of the obtained differences, both trial and error data, were not significant at the .05 level.

6. There was no significant difference between the two samples in ability to learn successive brightness discrimination reversal problems. When compared with controls, operated rats did not show a disproportionate increase in trials or errors which might be attributable to increased perseverative interference. When the trial and error data of the operated group were expressed as percentages of the controls, it was seen that operated *S*s showed their greatest deficit on the original task. Reversal learning had the effect of lessening the differences between the two groups. Operated rats show evidence of "learning to learn" brightness discrimination reversals.

DISCUSSION

The results obtained from analysis of the data indicate that rats with frontal lesions were inferior to control *S*s in learning the original simple maze problem, but the differences were not statistically significant. Reversal learning of this problem, however, revealed significant differences between the two groups. Still greater differences were found when the two groups were compared for ability to reverse a more complex problem. We have borrowed Settlage's explanatory term "perseverative interference" to account for these differences. When compared with controls, rats with frontal lesions show increased perseverative interference as the complexity of the task is increased.

Although rats with frontal lesions are inferior to controls in ability to learn maze reversal problems, they are not significantly inferior in their ability to learn brightness discrimination reversals. Operated animals, while slightly inferior to controls, show evidence of "learning to learn" discrimination reversal tasks as do normals.

Several explanations may be advanced for the ability of frontal rats to learn discrimination reversals. The results found with the maze problem indicate that operated *S*s show greater deficit on complex problems. This suggests that a more difficult discrimination reversal problem, as presented by a multiple-discrimination apparatus, might be more difficult for operated *S*s than for controls.

A second possible explanation of these results is found in the nature of the problem being learned. The maze problem involved dependence upon definite motor cues, and it was the "motor" areas which were damaged. The discrimination problem did not involve such a dependence upon motor cues.

Lashley (14) suggested that brightness discrimination habits in the rat are mediated by subcortical centers. It may be postulated that habits of brightness discrimination reversal, as well as the original brightness discrimination learning, are mediated by subcortical centers. At least, the present study indicates that the specific brightness discrimination and discrimination reversal tasks used did not depend upon the integrity of the frontal cortex in the white rat.

The implication of these results is that reversal ability is not a separate, discrete, and specific ability which is dependent only upon the integrity of the frontal cortex. The ability to reverse also depends upon the task which is being reversed. If initial learning is dependent upon the integrity of the frontal lobes, reversal learning may be expected to be influenced by frontal damage. If the initial learning is not dependent upon the frontal lobes, reversal learning of that task need not be influenced by frontal lesions.

The suggestion that spatial factors may be especially affected by frontal lesions is in need of experimental verification. In the present study it was noted that the maze reversal habit, a habit depending upon motor cues and positional or spatial orientation, significantly differentiated operated rats from controls. An indication that similar results may be found in the human *S* is found in the reports of Porteus and Kepner (16) and King (9). These authors report that frontal lesions result in impaired ability to demonstrate the type of intelligence which is measured by the Porteus Maze, a test relying heavily upon spatial factors. Possibly tests utilizing spatial factors combined with reversal may be especially sensitive to frontal damage in the human *S*.

SUMMARY

The study was designed to investigate the effects of frontal lobe lesions upon habit reversal in the white rat. Two problems differing in their degree of dependence upon the frontal lobes were chosen. One of these, the habit of brightness discrimination, was not expected to be affected by frontal lesions. The reversal learning of this problem would likewise not be affected by frontal lesions unless reversal ability is dependent upon the integrity of the frontal lobes. The other problem, a maze problem, is dependent to a greater degree upon the brain areas which were destroyed. Animals with frontal lesions were expected to show deficit in reversal learning of this problem when compared with controls. If reversal learning of the brightness discrimination problem was not affected by frontal lesions, but the reversal learning of the maze problem was, it would suggest that deficit in reversal learning on the part of operated *S*s does not depend solely upon the integrity of the frontal cortex, but depends in part upon the type of problem which is presented.

It was also postulated that increasing the difficulty of the task to be reversed would result in increased perseverative interference for the operated *S*s when compared with their control litter mates.

The following conclusions appear to be justified by the results:

Rats with frontal lesions are not significantly inferior to controls in their ability to learn a simple maze problem. When the task is reversed, however, and they are forced to change their directional choice for reward, the differences between the two groups are statistically significant. The differences between the groups became greater when a more difficult maze task was presented. Operated *S*s show increased perseverative interference and a disproportionate difficulty, compared with controls, when complexity of the maze task is increased.

Operated and control *S*s were not significantly different in their ability to learn the initial brightness discrimination habit. When the task was reversed and the animal had to learn to choose the previously unrewarded stimulus, the differences between groups were still not significant. A second reversal decreased the differences obtained between the groups. Operated rats, as well as controls, show evidence of "learning to learn" brightness discrimination reversals.

The ability to learn the reversal of any given task does not appear to be necessarily associated with the integrity of the frontal cortex. Deficit on the part of operated animals in learning reversal problems depends upon the type of task which is presented.

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Received October 11, 1953.

A STUDY OF FIGURAL EQUIVALENCE IN THE PIGEON[1]

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It has been very well established that birds can differentiate visual figures quite successfully (2, 3, 4, 5, 7, 11, 15); very little can be said about the extent of transfer of a learned visual discrimination to other figures. If, as the work of Layman (11) seems to suggest, visual-figure discrimination learning in the bird is elaborated elsewhere than in the telencephalic cortex, the question arises as to whether or not the nature of the response transfer to figures varied from the original training figures along certain dimensions will be found to differ from the behavior of the mammalian *S*. This experiment represents an attempt to learn something of the nature and extent of transfer of an acquired visual-figure discrimination in the pigeon when the training figures are altered in various amounts with respect to the dimensions of rotation, cue reduction, size, distortion, and brightness, under the condition of a constant background.

METHOD

Subjects

Twenty-four two- to four-year-old, experimentally naive, domestic pigeons, ranging from 459 to 785 gm. in weight, were used. Individual living cages of 4 cu. ft. were provided, and each bird had visual access to several other birds. They were maintained on Albers Pigeon Mix and grit, with water always available. During the experiment, the birds were fed only in the training box with dried peas and corn. Each bird was handled by *E* daily, and daily weight records were kept.

Apparatus

The experimental apparatus consisted of a large fibreboard box containing a lighted training compartment in which *S* could be placed and observed by *E* via a one-way vision device. The stimulus figures were presented in this compartment, and a feeder projected into it just below the stimulus presentation windows. The animal was restrained from this wall by means of a large glass door placed 3.5 in. out. This door could be raised and lowered manually.

Figure 1 illustrates the floor plan of this device. The box was 28 by 35 in. at the base and 21 in. in height. The training compartment was 20 by 20 in. at the base, with a height of 15 in., by virtue of an elevated floor. All interior surfaces were white except for the lateral walls of the training compartment, which were of glass, backed by a double layer of white cheesecloth. The removable roof contained a centrally placed 3- by 10-in. milk-glass window with a 25-w. light 3 in. above it. This sole light source provided an evenly diffused lighting that tended to minimize shadows.

On wall *A* (Fig. 1) were two circular openings 2.5 in. in diameter and 3.75 in. apart from center to center. These openings were 7 in. from the floor to their centers, and were covered by a 4- by 9-in. sliding door. This door could be raised and lowered by hand. The stimulus figures were presented behind these circular openings.

A peck to the proper stimulus figure yielded a contact pulse of electrical energy which was led into a time-delay circuit, which in turn activated the feeder mechanism; this sequence required 0.9 sec. The feeder was centrally placed, 2 in. below the stimulus windows, and consisted of a rotating disc with ten cups, which had a capacity of 3 gm. of feed each.[2]

Training

Initially, each bird was placed in the training box for 10 min. every other day. They were no longer fed in their living cages, and food was available in the feeder cup of the training box. Each bird was trained to peck a striated pattern, and after 15 rewarded pecks to such a figure, the discrimination training was begun. The training schedule consisted of ten trials during a 10-min. session each day. A trial was defined as a single presentation of a pair of stimulus figures accompanied by one peck, whether this was rewarded or not. On each trial, the stimulus door was raised to expose the two figures. Three seconds later the large glass restraining door was raised, allowing a response. After one peck, the stimulus door was lowered. The *S* was allowed sufficient time to empty the feeder cup, if the proper choice had been made. Otherwise, the restraining door was also lowered immediately. Thus, the design was that of simultaneous discrimination learning by the noncorrection method. Training was continued until the criterion of two successive days of 100 per cent correct response was attained. During this time, new stimulus cards were substituted in order to avoid training to inadvertent cues on soiled cards.

The "random" order of presentation of triangle (positive) and square (negative) was subject to certain restrictions. Each daily block of ten trials included five trials with triangle in the left and five in the right position, and on no more than three successive trials

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[1] This paper is a condensation of the experimental portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the department of psychology at the University of Washington in 1953.

[2] This feeding device was designed and constructed by George Price, instrument maker of the department of psychology, University of Washington, for use with rats. It is readily adapted for use with birds.

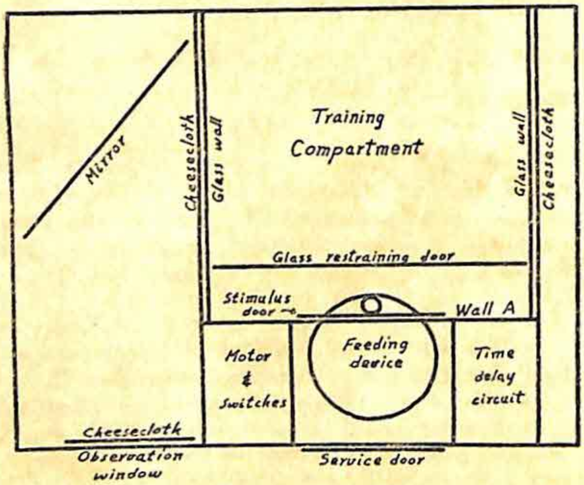

FIG. 1. Floor plan of the training box. The *S* is placed in the training compartment by means of an overhead door, and can be observed by *E* via the observation window and mirror. The stimulus cards are changed and the feeder is loaded through the service door. The restraining door and the stimulus door are manipulated by draw cords next to the service door.

could triangle appear in the same position. This allowed 192 possible ten-trial blocks, which were assigned to days by means of a table of random numbers. The tendency to assume a position habit made these restrictions necessary.

Testing

When the criterion of learning had been reached, the birds were then tested for equivalence responses during a four-day period. Each day, each animal received 5 training, 5 testing, 5 training, and 5 testing trials, in that order. Hence, each *S* received 20 trials on each of four testing days, and 40 pairs of testing figures were used. During the 10 training trials each testing day, the birds were rewarded only for correct choices. Reward was available for any choice on the test figures, although the amount was reduced to 2 gm. This rewarding of test trials was done to insure continued response.

Testing figures. The stimulus properties to be considered in studying visual-figure discrimination are at least six in number (1); only five of these were studied in this experiment: rotation, cue reduction, size, distortion, and brightness. The shape of the background was held constant. The training figures consisted of an upright equilateral triangle and a square, both 1 sq. in. in area. The testing figures consisted of variations on these two figures with respect to the dimensions mentioned above. The figures were painted with black tempera on 3- by 3-in. white, light-weight cardboard, and could very easily be placed into position behind the stimulus presentation windows. Thus, each figure appeared to *S* in a circular setting.

The order of presentation of the five stimulus dimensions and the pairs of figures within each dimension requires some discussion. Figure 2 shows that five series of stimulus pairs were used, but that two of these, Series A and C, consisted of only five pairs each. These two series were combined to form one group. Thus, one group, consisting of ten testing pairs, could be assigned to each test day. This allowed 24 possible orders of presentation of the four groups, which were assigned to the 24 birds by means of a table of random numbers. On days when Series A and C appeared, random selection determined which should be presented first. The order of presentation of stimulus pairs within each series was also determined by a table of random numbers for each *S*. Thus, each bird received a different order of the five series of stimulus properties and a different order of test pairs.

RESULTS

The total number of training trials required to reach the criterion of two successive days of 100 per cent correct response ranged from 280 to 660, with a mean of 473.3 trials. There was no initial tendency to respond consistently to one or the other training figure, and no consistent response to the negative training figure was observed in any *S*. Reinforcement on the test trials suggests that some increment in response strength to the figures to which response is made may aid in the building of a concept of class-form during the testing period. Such a process should yield a steady decrease in the number of errors on successive days of testing, an outcome which is not statistically apparent in the data. The total distribution of errors on the testing figures for successive days was 37, 46, 44, and 40; the hypothesis of a uniform distribution of errors over the four testing days, tested by chi square, was found tenable. Hence, if such a process played a role in this study, it was exceedingly minor insofar as the present analysis is concerned.

Figural equivalence score. The usual measure of the extent of transfer of an acquired visual-figure discrimination consists in the percentage of testing figures responded to "correctly," correct here meaning a positive response to that member of a pair which is judged as "the more triangular" by human observers. Stated in terms of per cent correct response, the birds ranged from 72.5 to 92.5, with a mean score of 82.6. This may be stated in a way that conveys a little more information, viz., in terms of chi-square probabilities. When the hypothesis of a 50:50 distribution of responses for each *S* on the 40 test pairs is set up and corrected for continuity, it is found that the response distributions of 23 birds yield

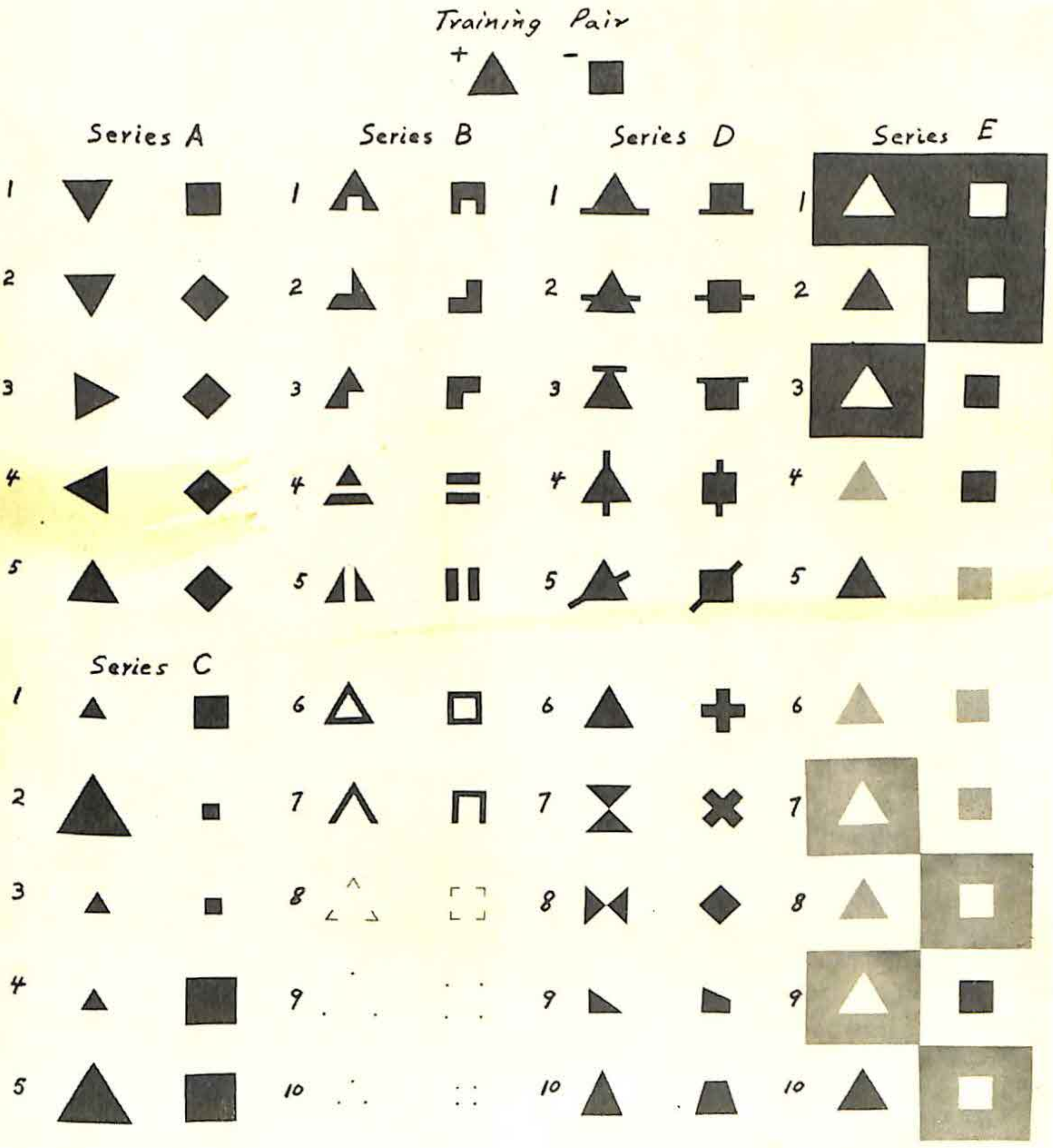

FIG. 2. The training and testing figures. Throughout, the left-hand member of each pair of testing figures is regarded as the "positive" member of that pair.

probabilities less than .001, and of one bird less than .01. This does not necessarily indicate, however, that all the "positive" figures were equivalent to the original triangle, and that what errors did occur were randomly distributed among the 40 pairs. On the contrary, some figures may, behaviorally, have been completely unrelated to the original training figures, and some "negative" test figures may have been equivalent to the original positive training figure. For this analysis, the performance of the 24 *S*s on each test pair taken separately is considered, and is presented in tabular form in Table 1.

Rotation. In Series A, failure of the differential response is quite evident. Only the triangle of pair A-5 was chosen by a significantly large number of birds. This finding is quite in agreement with that for the chick, when triangle and circle are used (2, 3, 13).

Cue reduction. On only the last two pairs of Series B, the dot figures, did the pigeons fail

TABLE 1

Corrected Chi-Square Values and Probabilities for the Distribution of Responses to Individual Test Figures

PAIR	NO.	CHI SQUARE	p (<)	PAIR	NO.	CHI SQUARE	p (<)
A	1	.000	1.00	D	1	22.042	.001
A	2	.375	.60	D	2	22.042	.001
A	3	2.042	.20	D	3	15.042	.001
A	4	3.375	.10	D	4	15.042	.001
A	5	18.375	.001	D	5	15.042	.001
				D	6	22.042	.001
B	1	18.375	.001	D	7	18.375	.001
B	2	22.042	.001	D	8	3.375	.10
B	3	22.042	.001	D	9	7.042	.01
B	4	15.042	.001	D	10	22.042	.001
B	5	22.042	.001				
B	6	15.042	.001	E	1	9.375	.01
B	7	18.375	.001	E	2	22.042	.001
B	8	5.042	.05	E	3	3.375	.10
B	9	.375	.60	E	4	1.042	.40
B	10	.375*	.60	E	5	22.042	.001
				E	6	22.042	.001
C	1	7.042	.01	E	7	.042*	.90
C	2	22.042	.001	E	8	15.042	.001
C	3	18.375	.001	E	9	18.375*	.001
C	4	1.042	.40	E	10	18.375	.001
C	5	22.042	.001				

* Distribution reversed.

to differentiate the triangular figure. Apparent "neurotic" behavior (hesitation, vacillation, withdrawal, rigidity) was observed when pairs B-8, B-9, and B-10 were presented. The widespread transfer of response to incomplete figures and outlines is quite in keeping with the general findings in mammalian figural equivalence studies (1, 9, 10, 14, 16).

Size. Like most mammals (1, 6, 8, 14, 16), the pigeons continued to respond to the triangle when, in Series C, the absolute and relative size of the triangle and square were altered. A strong "preference" for the larger of two stimulus figures, however, was clearly evident.

Distortion. Of the figures in Series D, only pair D-8 was not differentiated by a significant number of pigeons. This extent of transfer to distorted figures is comparable to that which appears in rats and primates only after specific concept formation training (1, 6, 14). The pigeon responds quite readily to altered figures.

Brightness. Figure-ground brightness reversal yields a complex background, for the white interior of the box remains unchanged while the immediate surround of the figure is changed. Nevertheless, brightness reversal of both figures does not disturb the discriminatory transfer in the pigeon or in mammals (1, 16), except in the case of the rat (6, 10, 12). Altering the absolute brightness of both figures without changing the figure-ground brightness relation does not disturb the pigeon or the mammals studied (1, 10). Whenever the triangle appears in its original figure-ground relation, regardless of the absolute brightness, and is paired with a square other than the original brightness, the discriminatory response continues undisturbed. When only the absolute brightness of the triangle is altered, however, the discrimination breaks down. Apparently, the original brightness and figure-ground relation are dominant over a figural discrimination when the initial training does not involve a brightness difference.

CONCLUSIONS

This experiment concerned the nature and extent of transfer of an acquired visual-figure discriminatory response, and was designed to yield two measures of transfer: an over-all figural equivalence score for each *S*, and an equivalence measure for each figure of a pair of test figures as they related to the original training figure. Several conclusions are indicated by the data.

1. The extent of transfer of an acquired discriminatory response to visual figures is as great (or greater) in the pigeon as in the mammalian forms that have been studied.

2. This discriminatory response transfer is not based upon the class-form of the stimulus figures.

3. The original discriminatory response had its basis in an adient response to the triangle, and neither avoidance of the square nor response based upon direct comparison of the figures was implicated.

4. Pigeons transfer with great accuracy to incomplete figures and outlines, and to distorted figures, but fail to differentiate dot figures. This transfer is not based upon response to class-form or to specific shape, nor has any single stimulus aspect been found essential to successful transfer of response.

5. Change in the absolute size of the two stimulus figures does not disrupt the discrimination when the original training figures are of equal size. Pigeons do, however, show a distinct "preference" for the larger of two visual figures.

6. Absolute brightness alterations or figure-ground brightness reversals do not disturb the differential response. However, when the relative brightnesses are altered and one figure contains the original figure-ground brightness relation, despite its absolute brightness, differentiation is interfered with in a noticeable, measurable degree. Hence, patterning becomes dominant over a figural discrimination.

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Received October 14, 1953.

SPATIAL LEARNING IN THE CANARY

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The problem underlying the experiments described here can be stated as follows: Will a canary pull a platform (by means of thread) to a point that will make possible the retrieving of food from a suspended bin when the food cannot otherwise be reached? If the canary is successful, can the performance be generalized? As will shortly be realized, the aim of *E* was to adapt Köhler's box problem to the anatomical make-up of birds.

METHOD

Subjects

Two canaries 10 weeks old, and of the same clutch, were used, usually after a period of overnight food deprivation. The canaries had readily learned to tug on a thread attached to a food tray that was placed on runners outside the cage. Each bird received 100 reinforcements in hauling the tray within reach. The birds were considered to be ready for learning to haul a platform and thus retrieve suspended food. One bird completed all steps of the experiments, whereas the second bird failed in Step 1 and was discontinued. The reported results apply only to the first bird.

Apparatus

a. A hollow cardboard prism (height 2½ in.) with a short length of thread emerging from the center of the front triangular face was used. In order to enable the bird to "see" the food that was to be covered by the prism, one small window was cut out from the bottom of each face and affixed with Scotch Tape. The prism was sufficiently stable to serve as a perch.

b. A toy plastic truck was placed on tracks on a base 8 in. long. A dowel perch was set on top of the truck. The truck could be displaced by tugging on thread that emerged from one end of the base.

c. This was the same as *b*, except that threads emerged from both ends of the base; thus, the truck could be pulled in either one of two directions.

d. This was also the same as *b*, except that the base was 14 in.

e. This was the same as *a*, but with a height of 1 in., and a hollow rectangular cardboard box ¾ in. high.

PROCEDURE AND RESULTS

1. Apparatus *a* was used to determine whether or not the canary could integrate in a single, smooth performance two habits: hauling the prism, and perching on the prism to reach the suspended food bin. To teach the first habit, food on the cage floor was covered by the prism. The bird, after "investigating" the prism, tugged on the thread and exposed the food. In the 35 trials that followed (in a period of 50 min.), the bird generally used a combination of tugging on the thread and pushing the prism from the rear. Since this habit was well established, training in the second habit was begun. The canary easily learned to perch on the prism and feed directly from the suspended bin. After 5 such free-feeding trials, the location of the bin was changed so that it could only be reached by displacing the prism. In its efforts to retrieve food customarily found beneath the prism, the canary positioned the prism under the suspended bin. Not finding food beneath the prism, it perched on the prism to obtain food from the bin. In a series of 25 trials the prism was brought within reach of the bin, and the canary obtained its reward. (During this series of trials the canary dropped its "looking" response for food beneath the prism.) Mechanical difficulties in moving the prism necessitated a change in apparatus.

2. Apparatus *b* was used. With the truck at one end of the base and the bin suspended 6 in. above the other end, the canary readily pulled the truck to a point below the bin, perched on the truck, and obtained its reward. After 10 successful trials the successful integration of the two habits seemed established. The question arose: Was the canary's tugging response stereotyped, or was it a response to the spatial relationship of the truck to the bin?

3. With apparatus *c*, the bin was randomly placed above one or the other end of the base, with the truck always at the opposite end. It took the canary 350 trials to master this problem. In the last 100 trials, the canary correctly tugged and positioned the truck 75 times. If at any time the canary tugged on the wrong end, the particular trial was scored as an error. At this point it occurred to *E* that the canary might have learned to tug on the same end above which the bin had been placed. Therefore, further trials were discontinued.

4. For a more decisive result, the bin was randomly placed at one of two points above the base—center and end (apparatus *b*). In all of 65 trials, the canary made no errors of overshooting the bin. In three of these trials, the canary jumped prematurely, after which it immediately resumed its tugging.

5. Since the displacement of the truck was not measured and the number of tugs required to position the truck was not counted, Step 4 was repeated quantitatively (apparatus *d*). The bin could now be randomized at three points above the base. In the predetermined 100 trials (24 trials at each point, and 28 interspersed trials in which the bin was placed directly above the truck), the canary made only one error of overshooting the bin. The object of the interspersed trials was to see whether or not the canary would tug when tugging was unnecessary. In all such interspersed trials the canary perched directly, without tugging. Moreover, each of three mean distances that the truck was displaced corresponded to the actual bin distances; the mean number of tugs required to position the truck was proportional to the actual distance. Apparent "judging" behavior occurred in 41 trials: after having tugged insufficiently, the canary would alternatingly "look" at the truck and bin from its tugging position or from a position intermediate between the truck and bin. Having "judged," the canary resumed its tugging. Moreover, it was observed that the canary frequently interrupted its tugging (by drinking, chirping, etc.) and then proceeded to position the truck.

6. To test for the generality of the canary's performance, Step 5 was repeated, after a vacation of four days, with nine randomized bin positions. The results were completely in accordance with those of the previous experiment.

In these experiments it may be concluded that the canary's truck-hauling activity is a response to the spatial relationship of truck to bin: As the spatial relationship of truck to bin is varied from trial to trial, so is the canary's tugging response; and if tugging is unnecessary (as with the interspersed trials), the canary does not tug. Moreover, on the response side, the fact that the canary can vary its behavior (stance at tugging position, interruptions in tugging, the number of tugs to get the truck to a given position, and premature perching followed by immediate resumption of tugging) and still appropriately position the truck provides further evidence that the "perception" of spatial relationship is the critical variable.

In another series of experiments, the attempt was made to teach the canary to stack a prism and a box in order to reach the bin, which was too high for either (apparatus *e*). The canary readily learned to retrieve the prism from any point in the cage and place it under the suspended bin, thus obtaining its reward. In addition, the canary learned to place the prism on the box, which had been fixed in position directly beneath the bin. (These results further bolster the interpretation of the canary's performance in the preceding experiments in terms of its response to spatial relationships.) However, in the crucial trial, when both prism and box were out of position, the canary seemed to be unable to stack them in a meaningful way. Actually, the canary did stack prism and box appropriately in only 10 of 100 trials; these results, however, may be due to chance. The fact that the canary did sometimes succeed may serve to indicate that, under appropriate conditions, with mechanical difficulties removed, the required task might be learned.

SUMMARY

A canary learned to retrieve food from a suspended bin, otherwise inaccessible, by: (*a*) positioning a toy truck, (*b*) positioning a small box, and (*c*) hoisting a small box on a larger box, the position of which had been fixed beneath the bin. These results supply evidence for a perceptual interpretation of the canary's performance.

Received August 19, 1953.

PERCEPTUAL DOMINANCE IN DISCRIMINATION LEARNING BY MONKEYS[1]

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Lashley (2, 3) trained rats to discriminate stimuli differing in multiple dimensions, and found, in subsequent critical tests to determine the basis of the discriminative response, that *S*s had been responding to differences in single dominant dimensions. He has elsewhere (4, p. 82) indicated that perceptual dominance affects discrimination learning by monkeys: "If a monkey is trained to choose a *large* red circle and avoid a *small* green one, he will usually choose any red object and avoid any green, but will make chance scores when like colored large and small circles are presented." This observation suggests that in monkeys, as in rats, only the dominant cue difference is associated with differential response when *S*s are trained to discriminate between stimuli differing in several dimensions.

The present investigation was planned to determine the role of perceptual dominance in discrimination learning by monkeys. With a method similar to that described by Lashley, *S*s were tested on a series of 15-trial discrimination problems. During the first six trials of every problem, the paired stimuli differed in color, form, and size. Following the sixth trial, the difference in one or two of these dimensions was eliminated, and testing was continued for nine additional trials, with reinforcement of appropriate responses to the remaining cue or cues. Six conditions could prevail in the last nine trials, and these conditions may be identified by the cue or cues which are retained after cue reduction, i.e., the differences retained were in color (C), form (F), size (S), color and form (CF), color and size (CS), or form and size (FS).

METHOD

Subjects. Four normal rhesus monkeys (no. A-17, A-20, A-22, and A-28) were studied in this experiment. The *S*s had been thoroughly tamed and had previously served in a study of experimental extinction. Since no monkey had been trained on more than four discrimination habits, the group may be considered essentially naive with respect to learning set formation.

Apparatus. The Wisconsin General Test Apparatus (1, Fig. 1) was used in this study. The construction and standard procedures for the use of the apparatus have been described in earlier publications.

Stimuli. Two hundred different stimuli were prepared for this experiment. Each was one of ten regular geometrical figures (trapezoid, semicircle, circle, star, hexagon, rhombus, square, rectangle, triangle, and cross) cut from ¾-in. plywood. None of the 20 copies of the different forms was identical with any other; one half were 4.5, and the remaining half 9.0 sq. in. in area. At each size, in turn, each of the identical forms was painted one of ten different colors (black, white, red, green, blue, yellow, purple, chartreuse, pink, and brown).

There were 2,025 different possible combinations of color and form differences. From this large population of potential problems, 96 pairings were randomly selected for testing during the problems prior to cue reduction. No combination was repeated.

Procedure. Each of the series of 96 15-trial problems consisted of two parts. During the first 6 trials, the stimuli differed in color, form, and size, e.g., a large blue trapezoid (+) versus a small green circle (−). New stimuli introduced between trials 6 and 7 reduced the number of relevant cue differences available during trials 7 to 15. To continue the example above, the stimuli might be changed to a small blue trapezoid (+) versus a small green circle (−), CF differences being retained. The six categories of cues retained after cue reduction (CF, CS, FS, C, F, and S) each recurred 16 times in random sequence during the experiment.

Three problems were tested each day for 32 days. No color, form, or size was consistently rewarded or nonrewarded, so there was minimal opportunity for interproblem transfer.

The 96 problems were divided into four blocks of 24 problems, each in order to test the significance of interproblem learning.

RESULTS

Since separate analyses of variance based on the pre- and postcue reduction portions of the problems failed to indicate any significant degree of learning set formation, the results of the entire experiment are summarized in Figure 1. The intraproblem learning curves presented in this figure show performance in discriminating stimuli differing in the three

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[1] This work was conducted at the Radiobiological Laboratory of the University of Texas and the United States Air Force, and was supported (in part) by funds provided under Contract AF 18(600)–165 with the USAF School of Aviation Medicine, Randolph Field, Texas.

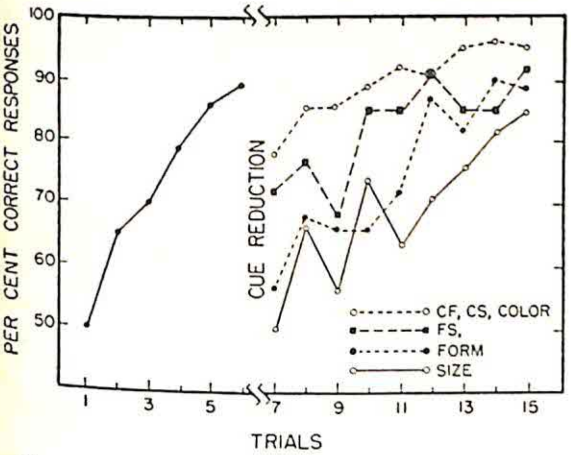

FIG. 1. The effect of combining stimulus cues upon intraproblem learning

dimensions (trials 1 to 6), and also the effect of cue reduction on discriminative performance (trials 7 to 15). Analysis of variance reveals that the six problem categories tested after cue reduction varied significantly in discriminability ($F = 17.46$, $p < .01$ with 5/45 *df*). Tukey's gap test, summarized in Table 1, indicates that the six categories represent four significantly different levels of difficulty. Color, CF, and CS do not differ significantly from one another in discriminability, and all are superior to FS, F, and S. Form and size differences are more easily discriminated than differences in form or in size, and F is in turn superior to S. Since the differences among the CF, CS, and C categories are irregular and not significant, the mean values for these three categories are plotted in Figure 1.

Inspection of Figure 1 shows that in the case of every type of discrimination, cue reduction depressed the level of performance on trial 7. The number of correct responses on the C, CF, and CS discriminations averaged 6.5 per cent less than on trial 6, and performance on the FS, F, and S problems dropped 17, 27, and 39 per cent, respectively. Trial 7 performance on the latter three categories was not significantly better than chance. Intraproblem learning was rapid, however, and performance on trials 7 to 15 was significantly better than chance on all problem categories. The rates of intraproblem learning on the several classes of problems continued to differ throughout; the ranking of the problem categories was maintained on trial 15, although the differences among the categories in relative discriminability had decreased appreciably.

TABLE 1

Tukey's Gap Test of the Significance of the Differences between Mean Errors on the Cue Categories

CATEGORY	MEAN ERRORS	GAP*	p
CS	12.25		
		5.25	
C	17.50		
		1.25	
CF	18.75		
		8.00	.01
FS	26.75		
		10.00	.01
F	36.75		
		8.25	.01
S	45.00		

* For .05 level of confidence, gap = 5.29 with 15 *df*; for .01 level of confidence, gap = 7.29 with 15 *df*.

DISCUSSION

In general, the results of the present experiment agree with those obtained in previous investigations (5, 6, 7) of the relative discriminability of stimulus dimensions for the monkey. The rank order is identical in all four studies: color differences are most easily distinguished, and form and size, form alone, and size alone are progressively more difficult. The results of the present investigation differ from those reported in the earlier papers, however, in finding that size differences were significantly less discriminable than form differences and that differences in form and size are significantly more discriminable than differences in either form or size alone.

Regarding the concept of perceptual dominance, tested in this experiment, the following observations support the hypothesis: Differences in CF and CS were not significantly more discriminable than differences in color alone. Performance on those problems which required differential responses to nondominant cues (F, S, and FS) was not significantly better than chance on trial 7, and continued to be inferior to performance on problems in which the dominant cue was relevant throughout trials 7 to 15.

The following results, however, fail to support the hypothesis that monkeys associate differential responses with only the dominant relevant cue: Performance on all categories was significantly better than chance, and the level of performance attained on F, S, and FS problems was approaching the level attained on the color categories by trial 15. Although form was "dominant" over size, the combination of form and size differences facilitated discrimination.

It may be argued that the conditions of the present experiment induced in *S*s a set to respond to all three relevant cues during the first six trials in anticipation of the subsequent, random cue reduction, and that presentation of many problems is not an adequate method of testing for the logical consequences of the hypothesized construct, perceptual dominance. Whether the tendency of the monkey to learn the significance of differences in more than one dimension was learned in the context of this experiment or elsewhere is not, however, important. The significant datum is of comparative interest—monkeys, in contrast to rats, base their discriminative response to stimuli varying in multiple dimensions, at least in part, upon all the relevant differences that differentiate the stimuli.

SUMMARY

Four rhesus monkeys were tested on a series of 96 15-trial discrimination problems. During the first 6 trials of every problem, the stimuli differed in color, form, and size. The number of relevant cues was reduced on trials 7 to 15 by the elimination of the differences in one or two of the dimensions. Six types of problems (CS, CF, FS, C, F, and S), named for the relevant cue or cues that were retained throughout trials 1 to 15, were tested 16 times each.

The following results were obtained:

1. Performance scores were depressed, on all types of problems, on the trial after cue reduction. Only on those problems in which a difference in color was present was trial 7 performance significantly better than chance.
2. Significant differences in performance were observed among the different types of problems; problems involving color differences were significantly more discriminable than FS, F, and S. The latter three differed significantly among themselves.

The data indicated that, although perceptual dominance has some effect on discrimination learning by monkeys, monkeys, in contrast to rats, learn the significance of all relevant stimulus cues.

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Received November 18, 1953.

DIFFERENTIAL FIRST-TRIAL PROCEDURES AND DISCRIMINATION LEARNING PERFORMANCE[1]

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Any attempt to account for the progressive improvement in the learning of successive discrimination problems (formation of learning sets [1]) must specify the roles of two general classes of factors: (*a*) the acquisition of the ability to differentiate the stimuli, and (*b*) the development of the ability to utilize such a stimulus difference to secure a reward. Clearly, the slope of the learning curve will be determined by the slower of these two factors. If, as Nissen suggests (4), the perception of a difference is immediate, then experimental effort should be directed toward an analysis of roles played by supporting habits, irrelevant habits, and interproblem transfer tendencies (5). The present experiment examines the effects of four different methods of denoting the correct stimulus object on the first trial upon the subsequent acquisition of the problem. While emphasizing the utilization-of-information factor, this experiment also provides an estimate of the naive monkey's efficiency of stimulus differentiation.

METHOD

Twelve monkeys participated in the experiment. All were naive with respect to formal discrimination training. They were tamed, however, and they were trained to displace a single object from a food well to secure food.

Except on the first trial of each succeeding problem (which defined the experimental treatments), all animals were treated alike. The entire experiment was conducted with a modified version of the Wisconsin General Test Apparatus (1). In this device the caged monkey faces two stimulus objects that cover food wells in a retractable gray tray. The animal is allowed to displace one object to secure food.[2] The critical facts to be noted were: (*a*) simultaneous discrimination; (*b*) blind baiting; (*c*) two-choice, object-quality discrimination; (*d*) food reward for correct choice (trials 2 through 6); (*e*) noncorrection procedure.

Each problem lasted for only six trials. As soon as a problem was completed, a new problem was introduced. Ten problems were administered daily until the animals had completed 250 problems, which constituted the first phase of the experiment.

The 12 animals were assembled into four groups of 3 animals each. As noted earlier, the difference among groups involved only the first trial of each problem.

Group Food (+). No matter which object the animals chose on the first trial, they obtained a raisin or peanut reward. This choice defined the "correct" object. Its selection, and only its selection, could secure food for the animals on subsequent trials.

Group Marble (+). No matter which object was chosen on trial 1, its removal from the food well uncovered a marble. This choice also determined the correct object of the problem, and its selection on subsequent trials secured food for the animals.

Group No Food (−). The first trials for the animals of this group were invariably "wrong." The monkeys found only an empty food well under the object of choice. On subsequent trials they had to select the *other* object to secure food.

Group Marble (−). The animals of this group, like those of Group Marble (+), invariably uncovered a marble on trial 1. Unlike that group, however, the members of Group Marble (−) had to select the other (nonpreferred) object on subsequent trials to secure food. In this respect their obligations were like those of Group No Food (−).

In the second phase of the experiment all animals were administered 50 problems according to standard learning set procedure (1). In essence, the success of the response on the first trial is determined by chance. The correct (rewarded) object is determined by a predetermined scheme, and the animals must discover which of these objects covers the food. Trials 2 to 6 follow according to the previous plan.

RESULTS

The four panels of Figure 1 portray the progressive changes occurring in intraproblem learning over successive blocks of 50 problems each. The following observations can be made with respect to this figure. (*a*) The confirmation of a preference by either a marble or food on the first trial leads to significantly better than chance scores on trial 2 throughout the experiment. (*b*) Intraproblem learning curves for the Food (+) and the Marble (+) groups are practically flat, and the slopes change relatively little over successive blocks of problems. (*c*) The Marble (+) curve is higher than the Food (+) curve. (*d*) Progressive

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[1] Supported in part by a research grant (M-359) from the National Institute of Mental Health of the National Institutes of Health, Public Health Service.

[2] Detailed descriptions of apparatus and test-trial procedures and complete summaries of the analyses of variance are available from the authors.

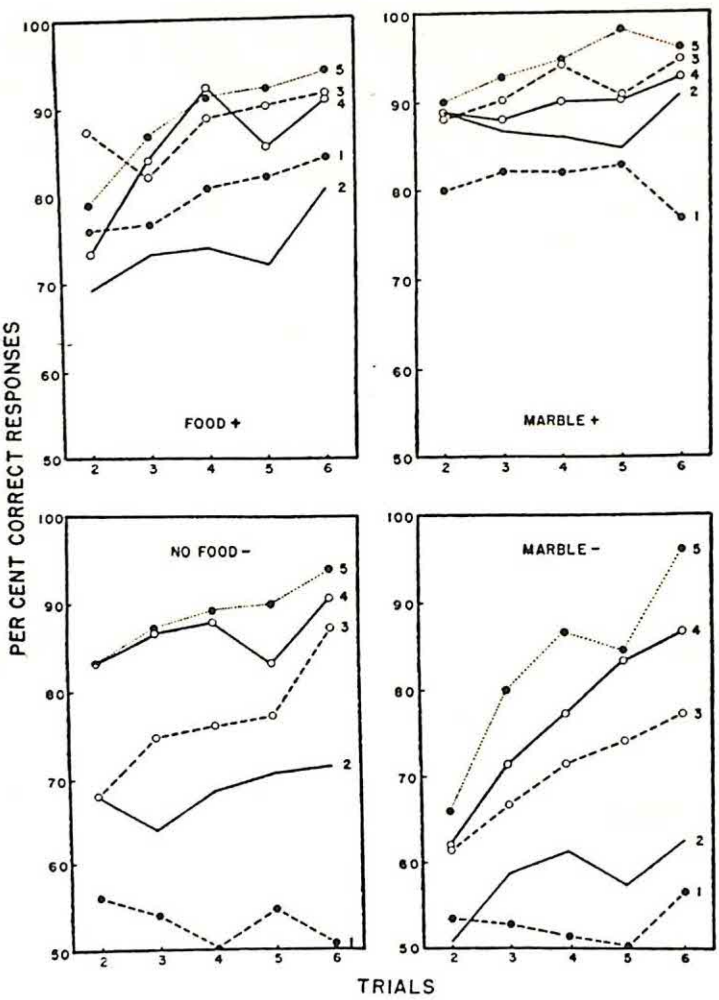

FIG. 1. Intraproblem learning curves for each group based on five successive blocks of 50 problems each

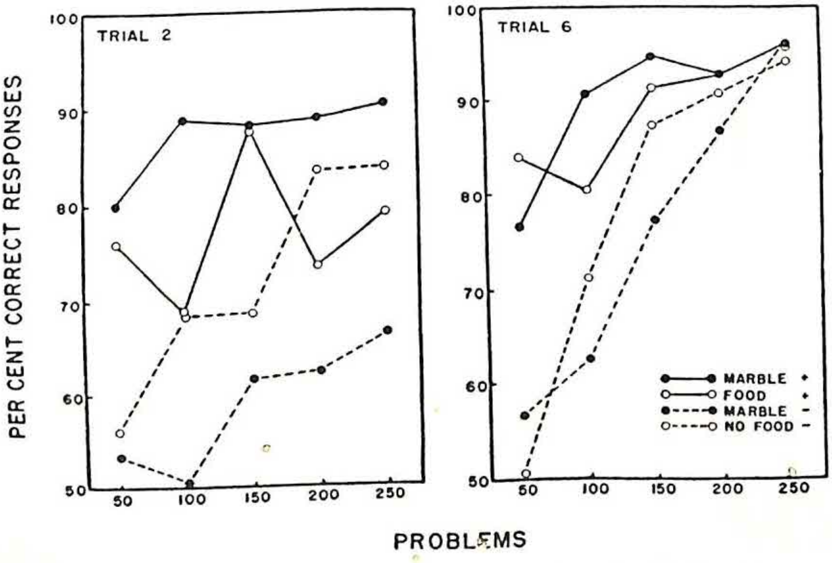

FIG. 2. Interproblem learning curves (learning set curves) for trial 2 and trial 6 performances of each group

steepening of the intraproblem (trials 2 to 6) learning curves occurs only in the Marble (−) group. (*e*) Performance during the first 50 problems of the No Food (−) and the Marble (−) groups is consistently near a chance level.

These observations are supported by the analysis of variance, the most important item of which was the trials × problems × groups interaction based on 48 *df*. This item was significant at the .01 level of confidence when tested against the trials × problems × animals within groups interaction term based on 128 *df*.

The two panels of Figure 2 show interproblem learning curves (learning set curves) for trials 2 and 6 for each group. From the data for trial 2 in this figure it is seen that the Marble (+) curve is highest and the Marble (−) curve is lowest. From the right panel of this figure it can be seen that whereas the two (+) groups initially are superior to the two (−) groups, these differences disappear by the end of the experiment. By comparing the two panels we may also note that in every case the learning set curve for trial 6 is steeper than the corresponding curve for trial 2.

Since under the procedures for phase 2 the animals for the first time encounter both correct and incorrect first trials, it is now possible to compare the performances on trials 2 to 6 following a correct initial trial (+ curves) with those following an incorrect initial trial (− curves). The data are plotted for each group in Figure 3. The four panels of the figure portray the percentages of correct responses on each trial for the two kinds of problems. The data are based on 50 problems approximately uniformly distributed between (+) and (−) problems.

Inspection of this figure reveals the following: (*a*) For the Food (+) and the Marble (+) groups, performances on trials 2 to 6 that follow a correct initial trial are superior to performances that follow an incorrect initial trial. (*b*) For the No Food (−) and the Marble (−) groups, the performances following an incorrect trial are at least equal to and possibly superior to performances following correct first trials. (*c*) It is at least as easy for Group Marble (−) to reverse an initial incorrect response as it is for Group Marble (+) to repeat an initial correct response. (*d*) Over-all performances of the four groups, based on both (+) and (−) problems, are practically equal.

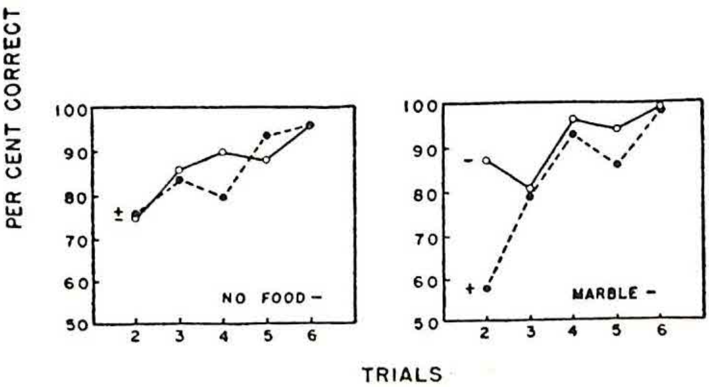

FIG. 3. Comparison of performances on trials 2 through 6 following a correct first trial and following an incorrect first trial. All data are based on a series of 50 problems inserted after completion of the first (differential treatments) phase of the experiment. Panel labels refer to experimental treatments during first phase of the experiment.

A number of comparisons may be made between this figure and Figure 1. (*a*) Note the (+) curve (Fig. 3) for Group Food (+); it is practically identical to the top curve for the same group in Figure 1. (*b*) A similar comparison for Group Marble (+) shows that the performance represented in Figure 3 is inferior to that shown in Figure 1. That is, food reward is less effective than its surrogate. (*c*) The (−) curve for Group No Food (−) is essentially unchanged from the top curve shown for the same group in Figure 1. (*d*) The (−) curve of Figure 3 for Group Marble (−) is clearly superior to the top curve of Figure 1 for the same group.

DISCUSSION

A number of detailed results have been presented that appear to have implications for three broad theoretical problems. The first of these deals with the stimulus differentiability of the naive monkey. The data of this experiment have shown that under favorable conditions consistently high discrimination test performance can be obtained from the beginning of training. Such a finding, of course, is consistent with the hypothesis that differences in stimulation are immediately perceived (4). It also argues against the necessity of the gradual development of certain facilitating responses before proficient stimulus differentiation can occur.

The second general problem deals with the comparative importance of food as a reward and as a signal on trial 1 for discrimination learning and the formation of learning sets. Related to this problem is the universality of such parameters throughout the learning experience of the animal. The data of this experiment as well as those of another report (5) show that food reward for an initial response is very likely to elicit a repetition of that response in inexperienced animals. After the animal has had experience with several hundred problems, an unrewarded response is more often followed by a correct response than an initial correct response (3, 5). Thus, the importance of food reward for the elicitation of correct responses is seen to diminish with extensive discrimination test experience. Furthermore, the equality, if not superiority, of the marble over food as a signal to repeat a correct response further questions the significance of food reward for learning.

The third general area for which these results have implications deals with the significance of stimulus preferences in discrimination learning. The training during the extensive first phase of this experiment was such that for two groups (Marble [+] and Food [+]) reward coincided with the preference, whatever the basis of the preferences. For the other two groups (Marble [−] and No Food [−]) the initial preferences had to be suppressed. Despite these long-lasting differences, when tested on a series of problems under identical conditions, the over-all efficiencies in performance of all groups were the same. Groups which were trained to perseverate a preference quickly learned to suppress a nonrewarded preference. Groups which had experience in suppressing a nonrewarding preference had only little difficulty in perseverating a reward preference. That the performances on the standard problems were essentially equal, even though these problems differed somewhat from those previously experienced, probably indicates the general deterioration of preferences and their reduced significance in response determination. Insofar as these preferences are due to the transfer of previous associations of similar stimuli with food, these results are consistent with the concept of transfer suppression (5).

SUMMARY

Four groups of naive rhesus monkeys were tested on a series of six-trial object-quality discrimination problems. All animals were treated alike on trials 2 through 6 of each problem. The groups differed, however, in terms of the nature of the first trial on each problem. One group received food on its first choice and continued to receive food reward if the animal repeated his selection on the remaining five trials. Another group was treated like the first except that a marble was found under the selected object on trial 1. A third group found no food under its initial selection but obtained food on trials 2 through 6 if it selected the other object. The fourth group similarly had to reverse its initial choice, but the cue for this reversal was a marble. The results showed that the confirma-

tion and subsequent reward of an initial preference leads immediately to consistently high test performances. Reversal of an initial response becomes increasingly proficient with extensive training. Interproblem learning curves for the various groups differed markedly, and the nature of the difference depended upon which trial was considered. Subsequent testing on a series of problems according to the standard procedures revealed comparable differences. These results were interpreted in terms of the immediate detection of stimulus differences, in terms of the significance of food reward for learning, and in terms of the importance of stimulus preferences in discrimination learning.

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Received November 7, 1953.

INTENSITY, DURATION, AND REPETITION OF HEDONIC PROCESSES AS RELATED TO ACQUISITION OF MOTIVES

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The present study aims to test objectively the hypothesis that hedonic processes are the basis for acquisition of motives (7). To eliminate primary needs and drives we kept an unlimited supply of food and water in the rat cages at all times. Our animals were neither hungry nor thirsty, nor were they depleted in any known way during the experiments.

For incentives we employed brief exposures of sugar (sucrose) solutions that differed in concentration, in duration of exposure to the rat, and in frequency of exposure. Sugar solutions of all concentrations are known to be acceptable to rats, and the level of acceptability in a brief-choice feeding situation varies directly with the logarithm of the concentration (8). It has been shown that higher concentrations are consistently preferred to lower throughout the entire range from zero (distilled water) to saturation. We have assumed that the *intensity* of hedonic process is positively related to the concentration of sugar solution and that the *duration* of a hedonic process is positively related, within limits, to the duration of the animal's contact with a solution. We have controlled the *repetition* of hedonic processes by varying the number of daily contacts in a series of trials. Throughout the experiment there was a single contact per day with a sugar solution.

EXPERIMENTAL CONDITIONS

Design of Experiment

Four concentrations of sucrose solution were employed with four corresponding groups of rats as follows: group I (2 per cent), group II (6 per cent), group III (18 per cent), group IV (54 per cent). These concentrations form a logarithmic series with equal steps. For each group there were three subgroups. The rats in the first subgroup were allowed 1 sec. of contact with the solution per run; the rats in the second subgroup were allowed 4 sec. of contact; the animals in the third subgroup were allowed 16 sec. Thus, all told, there were 12 combinations of concentration and exposure time.

In carrying out the experiment we worked with two batches of 24 rats each. All 48 animals were treated alike during the first part of the experiment, which consisted of 18 daily runs with 1 taste of sugar solution per day. After this the batches were treated differently. The first batch was used to study the effect upon performance of shifting the concentration of solution and the second batch to study the effect of shifting the exposure time. The experiment as a whole was planned so that when concentrations were shifted, exposure times were held constant for all rats; when exposure times were shifted, concentrations were held constant.

In the first batch there were 1 male and 1 female for each of the 12 incentive conditions. Since we found that the females ran significantly faster than the males, we employed only males in the second batch.

Preparation and Care of the Sugar Solutions

All sucrose solutions have been prepared and specified in terms of per cent concentration *by weight*, i.e., a 2 per cent solution contained 2 gm. of sucrose and 98 gm. of distilled water per 100 gm. of solution. In selecting four concentrations for the experiment we wanted the lowest value to be definitely above the preferential taste threshold of rats (0.5 per cent for sucrose) and the highest value to be well below the saturation limit (67.89 gm. of sucrose can be dissolved in 32.11 gm. of distilled water at 25° C.). The four concentrations that we finally selected (2, 6, 18, 54 per cent) are widely dispersed along the continuum of acceptability, and they are equally spaced in terms of log units.

All solutions were carefully prepared and kept at room temperature in storage bottles. Fresh solutions were mixed from time to time. At the start of a daily experiment a quantity of each solution was poured into a beaker and from the beaker into the glass cup of the apparatus.

Exposure Times

The exposure times of 1, 4, and 16 contact-seconds were arbitrarily chosen. We are reasonably certain that with exposures up to 16 contact-seconds the approach to satiation is not a factor of importance. We do not know, however, the extent to which sensory and affective adaptation might influence the rat's performance.

A cumulative timer was employed for taking time out when a rat was not drinking the sugar solution. During an observation *E* depressed a key as long as a rat was in contact with the sugar solution and released the key when a rat paused or left the cup to explore. When 1 or 4 or 16 sec. of contact had been accumulated, there was a sharp buzz that served as a signal for immediate removal of the solution from the feeding plate.

Apparatus

A ground plan of the apparatus is shown in Figure 1. It is a modification of the standard food preference

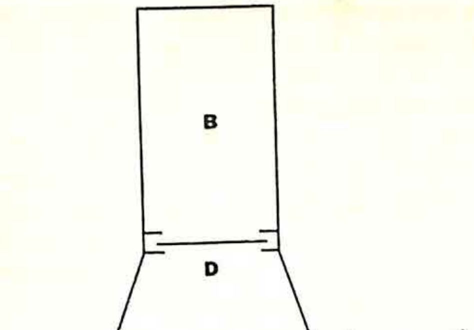

FIG. 1. Ground plan of apparatus

tester that has been described elsewhere (4). In general, the apparatus consists of a starting box (*B*) with door (*D*) leading to an open feeding plate on which a single foodcup (*F*) is located (at standard distance of 38 cm. from the threshold of the door). The cup (⅞ in. inside diameter) can be lowered from the feeding plate and raised by means of a lever device. The rat's behavior at the cup can be clearly observed through a Lucite window (*W*).

The duration of the rat's contact with a sugar solution was controlled by a cumulative timer. This timer, constructed by Merle Ridgley, contains a telechron motor that operates on alternating current but, to prevent lag, a rectified d.c. current is thrown into the circuit the instant the a.c. is turned off. The timer can be set for intervals of 1 or 4 or 16 sec.; when a total amount of time has been accumulated, a sharp buzz serves as a signal to *E* for immediate removal of the solution from the feeding plate.

Procedure and Measurements of Time

Each daily run was preceded by a delay of 60 sec. in the starting box and terminated by a pause of 60 sec. after the sugar solution had been lowered out of the animal's reach.

On each daily run the following time measurements were made: (*a*) The *latency* is the interval between raising the door and the instant the rump of a rat cleared the threshold of the door as seen in an overhead mirror. Latency was measured with a standard timer in hundredths of a second. (*b*) The *total time* (also called the *approach time*) is the interval between raising the door and first contact of a rat with the sugar solution. The total time was measured with a second standard timer in hundredths of a second. (*c*) The *running time*, obtained by subtracting the latency from the total time, is the time spent by an animal on the feeding plate after it has left the starting box and prior to contact with a solution. (*d*) The *over-all exposure time* is the time required for a rat to accumulate 1 or 4 or 16 sec. of contact with a given solution. Over-all exposure times were measured with a stop watch but have not been used in the present report.

Subjects

The rats were of Sprague-Dawley stock, 50 to 60 days old at the start of the experiment. They were weighed regularly and showed normal growth; they were healthy and active throughout the experiment.

To make certain that neither hunger nor thirst was a factor in the experiments, the rats were maintained upon an unlimited supply of Purina Rodent Chow and tap water. Their diet was adequate; we are aware of no need or deprivation of any kind. The only time the animals did not have access to food and water was for 30 or 40 min. during which they were put in carrying cages and given their daily runs.

Preliminary Habituation to Apparatus and First Experience with Sugar Solutions

Prior to the first trial the door to the starting box was locked open, and groups of rats were permitted to explore the entire apparatus. They were given 100 min. of preliminary exploration, 40 min. on the first day and 60 on the second. Following these two days the door to the starting box was closed and each rat was placed individually on the feeding plate. On the third and fourth preliminary days the cup was filled with a sugar solution of the concentration to be used with the particular rat. On the third of the preliminary days each rat was allowed to drink the solution for 30 cumulative seconds and on the fourth day for 30 additional seconds.

If, after 5 min. on the feeding plate, a rat had not accumulated 30 sec. of contact with the solution, a teacher rat was placed on the apparatus. The teacher ran immediately to the solution and started to drink; at this, the pupil invariably followed and drank. With slow rats this teacher technique greatly facilitated the accumulation of 60 sec. of preliminary contact.

It should be pointed out that in the preliminary period all rats had explored the total apparatus but that *only the feeding plate had been associated with the sweet taste* from a sugar solution.

RESULTS

Performance As Related to Concentration of Sugar Solution

Figure 2 shows the median latencies on trial 1 (upper curve) and on trials 14 through 18

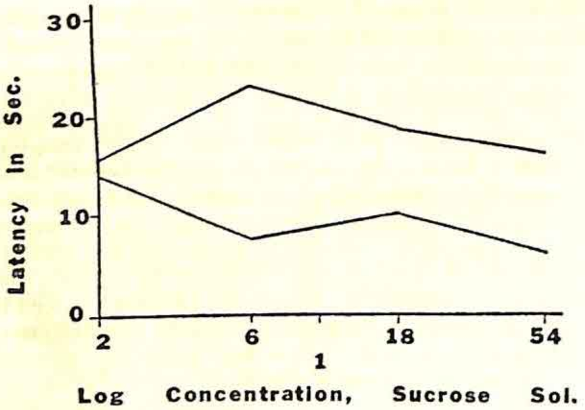

FIG. 2. Median latencies on trial 1 (upper curve) and trials 14 through 18 (lower curve) as related to concentration of solution (48 rats)

(lower curve). In the upper curve each point is a median based upon latency measurements of the 12 rats in each group. In the lower curve each point is based upon 60 latency measurements (12 rats, 5 days).

Figure 2 shows clearly that on trial 1 (upper curve) there was only a chance relation between time spent in the box prior to leaving it and concentration of the sugar solution that served as an incentive. After 14 to 18 daily runs, however, all latencies were reduced and a concentration gradient became clearly apparent (lower curve). The slowest approach time was for the 2 per cent solution and the fastest for the 54 per cent solution.

Figure 3 shows the running time, i.e., the time spent by a rat on the feeding plate after emerging from the starting box and before making contact with the sugar solution. The upper curve gives the median running time for trial 1 and the lower curve the median running time for trials 14 to 18, inclusive. As in Figure 2, each point on the upper curve is based upon time measurements for 12 rats and each point on the lower curve upon 60 measurements (12 rats, 5 days).

The striking features of Figure 3 are these: (*a*) On the first run the rats showed a marked concentration gradient of running time. They ran faster to the higher than to the lower concentrations. The significance of the differences in running time was determined by Wilcoxon's (5) unpaired replicates test and checked by his groups of replicates test. If group I (2 per cent) is compared with group IV (54 per cent), the difference is significant at better than the .01 level. If group I is compared with group III (18 per cent), the difference is significant between .01 and .02 level. If group I is compared with group II (6 per cent), the difference is significant at the .05 level. Comparisons of groups II, III, IV were not significant, however, at the .05 level. (*b*) With repeated trials all running times were shortened and they approached a common limit. After 14 to 18 days of running, the initial gradient had almost vanished.

To study further the effect of repetition upon running time, we plotted individual performance curves (omitted here). These curves demonstrate that rats approach their physiological limit of running time more quickly with the higher than with the lower concentrations of sugar solution. For example,

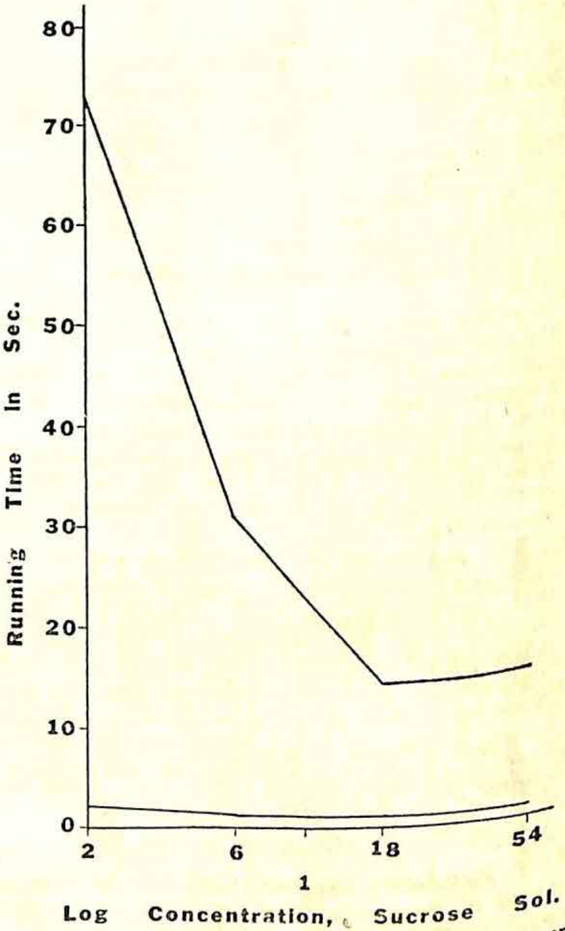

FIG. 3. Median running times on trial 1 (upper curve) and trials 14 through 18 (lower curve) as related to concentration of solution (48 rats)

TABLE 1

Relative Reduction in Latency through Repetition with 1, 4, and 16 Contact-Seconds with Sugar Solution

($N = 48$)

VARIABLE	DURATION OF CONTACT WITH SUGAR SOLUTION		
	1 sec.	4 sec.	16 sec.
Median latency on day 1	17.5	14.5	20.0
Median latency on days 14 to 18, inclusive	10.5	7.5	5.5
Reduction in latency	7.0	7.0	14.5
Relative reduction	40.0%	48.3%	72.5%

if we arbitrarily select, for purposes of comparison, a running time of 2.5 sec., then we find that group IV reached this running time on day 4; groups III and II reached this running time on day 8; group I reached it on day 11. Also, the variability within a group varies with concentration. Even after 14 to 18 repetitions group I remained the most variable and group IV the least; the other groups were intermediate in variability (as shown by the semi-interquartile ranges).

A point of theoretical interest that appeared in the individual performance curves for cumulative running time and also for cumulative latency is the following: Several of the rats in group I and one in group II showed little or no acceleration with repetition. Although the rats ran to the incentive solutions and tasted them, the curves showed little or no learning or only sporadic learning; there were well-marked plateaus in the curves. In groups III and IV, however, all rats yielded typical smooth learning curves with negative acceleration.

Performance As Related to Duration of Contact with Sugar Solution

The experiment was planned so that for each concentration four rats ran with 1 sec. of solution contact; four with 4 sec.; four with 16 sec. All told, there were 16 animals running for each of these exposure times.

The relative reductions in latency with repetition are given in Table 1. The table shows that on the first day of the series there was only a chance relation between latency and the duration of stimulus contact. The relative reductions with repetition, however, clearly

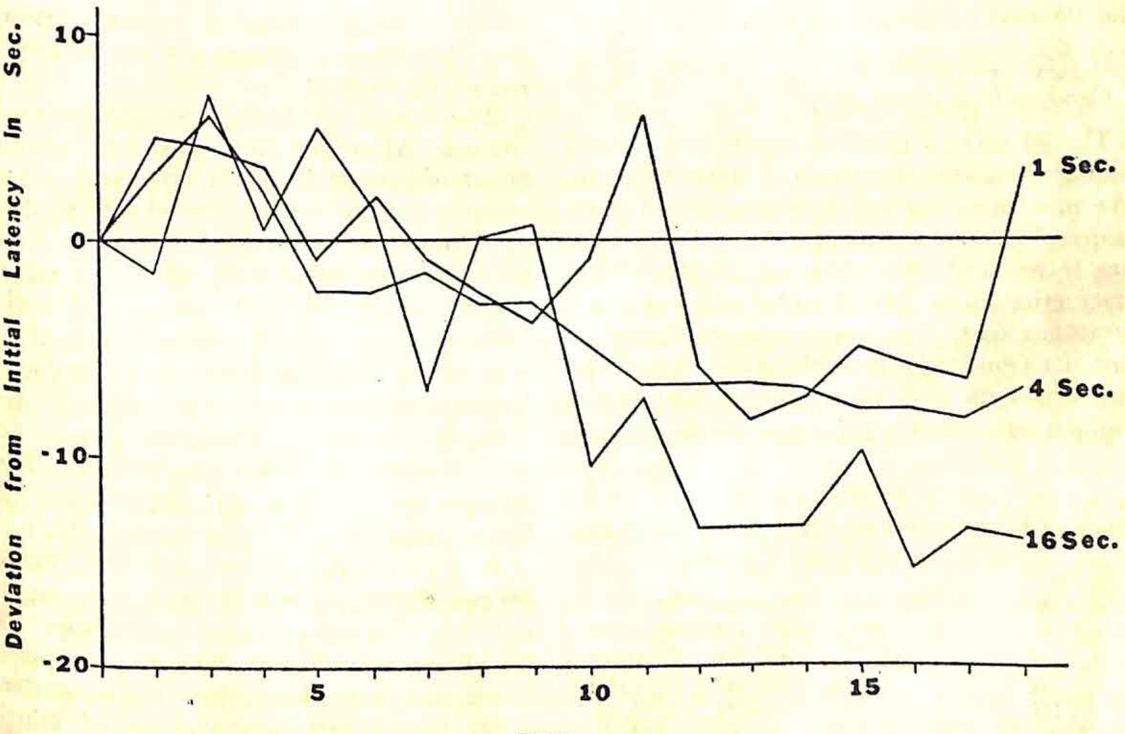

FIG. 4. Deviations of median latencies from initial latency with 1, 4, and 16 contact-seconds of exposure (48 rats)

indicate the greatest decrease for the 16-sec. group and the least for the 1-sec. group, with the 4-sec. group intermediate.

Figure 4 shows the deviation of median latencies from the initial latency as a function of the duration of contact with the stimulus solution. Each point on the three curves is based upon the measured latencies of 16 rats. The initial latencies are equated to reduce chance variations from group to group; the deviations from initial values, both positive and negative, are plotted for all 18 days in the first series of runs.

The data presented in Figure 4 clearly show the following: (*a*) For all groups there was an initial tendency to slow down for the first few days; this was followed by a speeding up of the time required for rats to leave the starting box. (*b*) For the first 8 or 9 days the three curves show considerable overlap with high variability and no consistent group differences, but after day 9, well-defined group differences developed. On the last 5 days of the series the 16-sec. group was clearly the fastest, the 4-sec. group intermediate, and the 1-sec. group the slowest. During the last 5 days the differences between groups are significant at the .05 level by Wilcoxon's test.

The Effect upon Performance of Changing the Concentration of Solution

The 24 rats in the first batch were tested with all four concentrations of sugar solution. The first incentive was employed for 18 days, as described above; on day 19 a new incentive was introduced. We have here regarded the first series as of 19-day duration on the assumption that a change of concentration on day 19 could not possibly affect the time measurements until after the rat had tasted the new solution. On this basis the first incentive was employed for 19 days, the second for 15 days, the third for 22 days (longer than the others, to counteract forgetting during the Christmas vacation), the fourth for 14 days.

TABLE 2

Relative Change in Approach Time (Total Time) after Shifts in Concentration of Solution

GROUP	1ST SHIFT	2ND SHIFT	3RD SHIFT
I	27.25	102.02	62.89
II	23.89	109.05	101.17
III	95.05	68.30	55.72
IV	100.48	69.85	173.12
Average range of change	72.20	36.46	77.84

The four successive concentrations of sugar solution for each of the groups are: group I: 2, 18, 6, 54; group II: 6, 54, 18, 2; group III: 18, 2, 6, 54; and group IV: 54, 6, 18, 2.

The data for individual rats are omitted to economize space, but we present in Table 2 some figures derived from the raw data through the following steps. First, for each rat individually we determined the median approach time (total time) for the last five days of running with a given incentive. There were, of course, four such medians for each animal. Second, for each rat individually we obtained an index of relative change. These indices were computed like percentages so that an index of 100 indicates no change in approach time; an index greater than 100 indicates a slower approach (longer time); an index less than 100 indicates faster approach (shorter time). Since there were three shifts of incentive, there are three indices of change for each animal. Third, the 12 individual indices of relative change for each group were averaged, and the group averages are the figures presented in Table 2.

The figures in Table 2 should be read as follows: After the first shift, the approach times of groups I and II (changed to higher concentrations) were speeded up while the approach times of groups III and IV (changed to lower concentrations) were less affected. After the second shift, groups III and IV (changed to higher concentrations) were speeded up while groups I and II (changed to lower concentrations) were slowed down. Similarly, after the third shift, groups I and III (changed to higher concentrations) were speeded up while groups II and IV (changed to lower concentrations) were slowed down.

When we interpret the figures in Table 2, we should remember that practice alone, without any change of incentive, should speed up all approach times. This normal practice effect was more than offset in five of the six shifts to a lower concentration of solution; and in one of these six there was only a slight speeding up of approach. In all shifts to a higher concentration, however, there was a marked and consistent speeding up of the rat's approach to the solution. In changing to a higher concentration the incentive effect and the practice effect reinforce each other.

To study the magnitude of changes associated with shifts of concentration, we averaged the two lowest indices of change and the two highest indices, and by subtraction we obtained the average range of a change produced by raising two concentrations and lowering the other two. The average ranges are shown in Table 2. It is interesting to discover that the average range of change in the second shift is about half that in the first and third shifts. Since in the second shift the concentrations were changed 1 log unit and in the first and third shifts 2 log units, we can conclude that: A shift in concentration of 2 log units produces, on the average, twice the amount of relative change in performance level as a shift of 1 log unit.

The Effect upon Performance of Changing the Exposure Time of Solutions

All animals of the second batch of 24 rats were given one trial daily for 21 days. On day 21 the group with 1 contact-second of daily exposure was changed to 16 sec.; the group with 16 sec. of contact was changed to 1 sec. Following these changes, rats in all groups were given daily trials until they completed a total of 38 runs. What is the effect upon performance of changing the duration of the rat's contact with a solution?

Table 3 summarizes the findings. The table shows the median approach time on days 17 through 21. Each median is based upon 40 time measurements (8 rats per group, 5 days). Beginning on day 21 and continuing through day 38 the contact times were changed for two groups. The median approach times for days 34 through 38 are shown in Table 3.

We should expect a change from 1 to 16 sec. to speed up the approach time and a change from 16 to 1 to slow it down. Both expectations were met, but the extent of the changes was surprisingly little. Although an increase in exposure time should speed up running, repetition alone (practice), without any change of exposure time, is known to have the same effect. It should be noted that the group with 4 sec. of contact and no change in exposure time made a much greater relative gain than the group changed from 1 to 16 sec. The change that we obtained in shifting from 1 to 16 sec., therefore, was much less than the change normally to be expected from practice alone!

TABLE 3

Relative Change in Approach Time (Total Time) after Shifts in the Duration of Contact

FIRST EXPOSURE TIME (sec.)	MEDIAN APPROACH TIME DAYS 17 TO 21, INCL.	SECOND EXPOSURE TIME (sec.)	MEDIAN APPROACH TIME DAYS 34 TO 38, INCL.	RELATIVE GAIN (%)
1	38.50	16	36.00	93.5
4	8.65	4	2.75	31.8
16	5.55	1	6.65	101.8

The change from 16 sec. to 1 sec. resulted in slowing down the approach time. In this instance the expected slowing down is opposed to the effect of practice. Actually the expected practice effect was more than offset by a reduction of exposure time.

Apparently the changes associated with shifts of exposure time are not as clear-cut as the changes associated with shifts of concentration. A further study is needed, therefore, to clarify the picture before a final conclusion upon shifts of exposure time can be drawn.

DISCUSSION

The Hedonic Basis for the Acquisition of Approach Motives

When it makes contact with a sugar solution, the rat continues to ingest it; if it pauses to explore, it returns for more. We assume that a positive hedonic process orients the organism toward the solution and builds up a tension that motivates return. Even a single sip of the sweet tasting solution must have an orectic effect, for after a single taste the rat returns from various positions and distances to taste it again.

From this point of view the data presented in Figures 2 and 3 raise a point of considerable psychological interest. On two days prior to the first run the rats had explored the apparatus for 100 min. with the door to the starting box locked open but with no sugar solution on the apparatus and no possibility of forming an association between stimulus cues from the apparatus and a sweet taste. After these two days the door to the starting box was closed. Since there was no possibility of forming an association between stimulus cues from walls, floor, and ceiling of the starting box and a sweet tasting fluid, we should expect no relation between *latency* (time required to leave starting box) and concentration on trial 1—and this is exactly what we found (Fig. 2). With repeated trials, however, a concentration gradient of latencies developed. This can be explained by assuming: (*a*) that the intensity of hedonic process is related to the concentration of sugar solution, and (*b*) that an approach motive is aroused by stimulus cues from the apparatus when the cues have been associated with the sugar solution in space and time.

The data presented in Figure 3 strikingly confirm this hypothesis. Prior to trial 1 each rat had tasted a sugar solution for 60 contact-seconds on the feeding plate (when the door to the starting box was closed). Hence, stimulus cues from the feeding plate aroused the approach motive as soon as the rat entered the feeding plate. On trial 1, as we might expect, there was already a well-marked concentration gradient of *running time*.

The present results agree with a previous finding that rats *run* faster to a preferred than to a nonpreferred food (6). The present results, however, indicate that with repetition of runs the animals approach a common physiological limit of running time. They approach this limit at different rates—the rate varying directly with the concentration of solution.

Our measurements of latency and running time do not correlate perfectly with solution concentration, for there are occasional inversions. In brief-exposure preference tests with sugar solutions, however, inversions were not found (8). This discrepancy may indicate that a brief-exposure preference test is a more reliable indicator of relative acceptability than measurements of latency and running time. It seems likely that inversions are dependent upon chance factors and that they would disappear with larger groups of *S*s and with the accumulation of more data.

In any event, the present experiment demonstrates that the strength of a learned sugar-seeking motive, as indicated by the time measurements of approach behavior, varies with three conditions: (*a*) the concentration of sugar solution, (*b*) the duration of contact with a sugar solution, and (*c*) the number of previous contacts. These three factors are independently variable. A change in one factor can readily be shown to be equivalent in its effect to some corresponding change in either of the other factors. Since these factors can be equated, they have a common denominator. This common denominator, we assume, is the degree of proprioceptive tension primarily aroused by the sweet tasting solution and secondarily aroused by stimuli from its surroundings.

Quantity of Reward versus Hedonic Processes

In experiments upon the quantity of reward, magnitude of reward has been varied in different ways. Quantity has been controlled by varying the number of food pellets offered (1), or the size of the visible reward (2), or, as in the present experiment, the concentration of the solution (3). In self-selection feeding experiments the gross quantity of a food ingested per day or per hour is tacitly assumed to measure its level of acceptability. It has been found, however, that relative acceptability measured by a brief-exposure preference test does not always agree with relative acceptability as determined by the quantity of food ingested (8). Preference (choice) and quantity of food ingested, therefore, are different operational criteria of acceptability, and the two criteria probably point to independent bodily mechanisms that regulate food acceptance. In the present experiment the quantity of reward has been varied by control of the concentration of sugar solution and by the duration of contact with it.

If we assume, for the sake of argument, that the quantity of sucrose ingested during 1 sec. of drinking a 2 per cent solution is unity, then the quantity ingested during 1 sec. of drinking a 54 per cent solution is 27 units, and the quantity ingested during 16 sec. of drinking a 54 per cent solution is 432 units. These relative quantities of sucrose are so far from agreeing with the relative changes in performance induced by variations of concentration, duration, and by repetition (Fig. 2, 3, 4) that we doubt whether *quantity* of reward is the correct basis for analysis of the data.

It seems better to interpret the data in terms of *affective* intensity, duration, and repetition than in terms of *quantity* of reward. On the basis of objective hedonic theory the present results are orderly and consistent. Further, an interpretation in terms of need reduction or drive reduction is out of the question since in the present work there was no initial need or drive to be reduced. Rather, the work describes the development of purposive behavior in the absence of a need or internal drive and with a maximizing, rather than minimizing, of the incentive stimulus.

Hedonic Processes and Learning

Studies of individual learning curves obtained with incentives of low hedonic intensity (2 per cent and 6 per cent sucrose solution) indicated that learning is not continuously present. During parts of the series of daily runs there was evidence of learning (practice gains), but during other parts of the same series there were plateaus and no indications of learning. This looks as if the effectiveness of an incentive in learning depends upon hedonic intensity. Our graphs suggest that there is a hedonic threshold for learning and that a rat may run to the solution without learning to run to it more quickly. If we assume that a rat is *motivated* on all runs, we cannot assume that it *learns* on all runs, for the facts are against this last assumption.

The facts make sense if we assume that there is a hedonic threshold that is not necessarily the same as the sensory threshold and that a hedonic process must be aroused before an animal learns to move toward or away from an incentive food object.

CONCLUSIONS

1. The speed at which rats approach a sugar solution, after brief daily tastes of it, is an increasing monotonic function of the concentration.

2. Occasional group-to-group inversions in the approach time, as related to concentration, suggest that approach times are less reliable as indicators of relative acceptability than the findings in brief-exposure preference tests.

3. If the concentration of a sugar solution is shifted, the time of approach is changed in accordance with the rule that rats approach a higher concentration (sweeter solution) more quickly than a lower (less sweet). The extent of change in approach time is related to the magnitude of the shift in concentration: a shift of two log units, up or down, being twice as effective in changing performance as a shift of one log unit.

4. The duration of contact with a sugar solution is positively correlated with the rate of approach to the solution. Rats practiced with 16 cumulative contact-seconds per day approach the solutions more quickly than those practiced with 1 contact-second. Rats practiced with 4 contact-seconds are intermediate in their rate of approach to the solutions.

5. The rate of approach to a sugar solution increases with the number of previous contacts with it. This fact can be interpreted in either of two ways: (*a*) in terms of the repetition of hedonic processes that organize behavior, or (*b*) in terms of the exercise of an instrumental act that is hedonically motivated.

6. In general, our experimental findings can best be interpreted by assuming that positive hedonic processes exist in the rat, that these hedonic processes organize approach motives, and that the strength of an acquired food-seeking drive is dependent upon the intensity, duration, and number of repetitions of hedonic processes. A food-seeking motive, we assume, is learned; and the act of running to a food is regulated by an inner determination that is aroused through environmental stimulus cues associated with the food.

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Received October 12, 1953.

A TEST FOR GENERALIZED SECONDARY REINFORCEMENT DURING EXTINCTION UNDER A DIFFERENT DRIVE

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Much recent experimentation has had as its aim the clarification of certain questions related to the nature and function of secondary reinforcement as a theoretical construct. Many of these questions have been confounded by the fact that secondary reinforcement as originally discussed by Hull (8) was defined by two different sets of experimental operations. The first is the case in which a secondary reinforcing stimulus is used to reinforce the learning of a new response in the absence of primary reinforcement (2), and the second is that in which the presence of the stimulus during experimental extinction leads to a greater number of responses than occur during its absence (1).

Estes (4, 5), utilizing the first of these two sets of operations, has reported that secondary reinforcement generalizes from one drive state to another. In the initial phase of his study an auditory click became the conditioned stimulus for animals under water deprivation to approach a tray, following which there was a reward of water. The animals were then divided into two groups, half being maintained on their original thirst drive and the others being transferred to a hunger drive. A bar which produced, when depressed, the same auditory stimulus previously associated with thirst, tray approach, and water reinforcement was next introduced. When the then thirsty or hungry animals were presented with this bar, there was no significant difference in the number of their bar-pressing responses even though the only reinforcement was that mediated by the auditory stimulus. Estes concludes that the effect of secondary reinforcement had generalized from the thirst to the hunger drive and had reinforced the acquisition of a new response.

If generalization is considered to be a failure to discriminate, as is suggested by the Gibson (6) generalization hypothesis, then training in which hunger and thirst drive stimuli are further differentiated could act to reduce the amount of secondary reinforcement that is generalized. Such a possibility gave rise to the hypothesis tested in the first of the experiments to be described, viz., will the amount of secondary reinforcement generalized under a different drive state be reduced as the result of previous drive stimulus differentiation?

It is clear from the experimental literature that rats are capable of being trained to make differential responses to the drive stimuli of hunger and thirst (8, 9). Training of this kind was therefore given to groups of rats which were then conditioned to an auditory click under food deprivation. At the time, the writers considered the second set of defining operations to be the more sensitive measure of secondary reinforcement. For this reason the animals were trained to make a bar-pressing response for food reward and were then extinguished under either food or water deprivation with only the auditory stimulus following each bar-pressing response. In this fashion it was thought that the hypothesis stated above was capable of being tested.

EXPERIMENT I

Method

Subjects. Twenty-three male and 13 female albino rats of the Wistar strain, 90 to 100 days old, were *S*s in the experiment.

Apparatus. A single-unit T maze elevated 37 in. from the floor was used for drive stimulus discrimination training. The alleys of the maze were 1¾ in. wide and their lengths were 36 in. from starting box to choice point and 18 in. from choice point to either goal box. The entire maze, including starting and goal boxes, was painted flat black. White cardboard doors were suspended at the entrance of each goal box.

A modified Skinner apparatus was used for the secondary reinforcement training and the measurement of generalization of secondary reinforcement. This consisted of a housing box with the usual horizontal bar activating, when pressed, a solenoid which discharged a single pellet from a food magazine. The bar was made of ⅛-in. aluminum rod and was 2 in. long. It required a force of approximately 5 gm. to displace it the ½ in. necessary to make the required contact. The interior of the box, 11 in. long, 8 in. wide, and 8 in. high, was painted flat black. Illumination of the interior was provided only by the normal room light passing through a 4½- by 4-in. plate of etched glass located in the ceiling of the box.

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[1] Now at The Ohio State University.

The secondary reinforcing stimulus was the auditory click of the solenoid which accompanied each bar depression.

Discrimination training. Prior to the beginning of drive stimulus discrimination training all animals were deprived alternately of food and water for five periods of 22 hr. each (WFWFW). Between each deprivation period they had both food and water present in their living cages for a 2-hr. period. The animals were then randomly assigned to two equal groups. One group was given discrimination training for a period of 24 days, while the other group was maintained during this period on its usual living routine (ad libitum food and water) except for daily handling to approximate that of the *S*s in the discrimination program. The discrimination training followed a fixed 8-day schedule, which permitted an equal number of food- and water-deprivation days. The length of each deprivation period, whether food or water, was always 22 hr. The schedule (FWFFWFWW) was repeated three times during the 24-day period. During the discrimination training food was always located in the left goal box of the T maze and water always on the right. The *S*s were given five self-corrective trials daily and permitted to eat or drink 10 sec. following entry into the goal box appropriate to their deprivation. The door to the other goal box was always locked. At the end of the discrimination training all *S*s receiving this training were responding 90 per cent or better to the side appropriate to the momentary deprivation.

Secondary reinforcement training. All *S*s received identical training in the bar-pressing situation. During this period, the motivating condition was 22-hr. food deprivation. On the first day *S*s were given four pellets. While *S* was eating the last of these pellets, another pellet was discharged by *E*. A total of six pellets was given in this manner. On the next day each *S* was placed in the box and permitted to press the bar to receive ten food pellets, and on each of the two following days was given 20 reinforcements following bar-pressing responses. A total of 60 bar-pressing responses was thus rewarded by single food pellets, with the discharge of a pellet always accompanied by the click of the solenoid.

Test of generalization. On the day following its last reinforcement each *S* was given an hour of experimental extinction with only the sound of the solenoid following its responses. The number of bar-pressing responses was recorded on a counter. During extinction half the *S*s of both discrimination-training and no-training groups were continued on 22-hr. food deprivation, while the other *S*s of both groups were transferred to 22-hr. water deprivation.

Results

The mean number of bar-pressing responses during extinction for each of the four groups is included in Table 1. It is apparent that there was a pronounced tendency for both discrimination-trained groups, food- and water-deprived, to respond more during the hour than the nontrained animals. The data of Table 1 also show a lack of evidence for the contention that secondary reinforcement has generalized from hunger to thirst for either discrimination-trained or nontrained animals. (Although the terms hunger and thirst are sometimes used in the present paper, they refer only to the fact that the *S*s being described are at that time in a scheduled period of food or water deprivation.) In fact, it appears clear that the presence of the secondary reinforcing agent during the extinction of those animals transferred from food deprivation to water deprivation had little effect on the total number of responses.

TABLE 1

Mean Number of Responses and Standard Deviations during One-Hour Extinction Period

GROUP	MEAN	*SD*
Discrimination training		
I. Food-deprived	313.1	95.5
II. Water-deprived	57.3	43.3
No training		
III. Food-deprived	210.8	119.0
IV. Water-deprived	22.3	17.3

The significance of the differences between mean number of responses is presented in Table 2. Because of the nonnormality of the sampling distributions, the raw data were transformed to logarithms for the purpose of applying tests of significance. The nonnormality likely results from the fact that such measures are restricted to zero at the lower end of the distribution but unrestricted at the upper end. The *t* ratios show that only the mean difference between the two food-deprived groups (I–III) approaches statistical significance. In all other comparisons, however, the null hypothesis may be safely rejected.

TABLE 2

Comparison of Mean Response Differences among Various Groups during One-Hour Extinction Period

GROUPS COMPARED	MEAN LOG DIFFERENCE	*t*	*p*
I–II	0.8185	6.243	< .01
I–III	0.2190	2.053	< .10 > .05
II–IV	0.4749	2.499	< .05 > .02
III–IV	1.0744	6.171	< .01

Discussion

The data do not lend support to the major hypothesis of the experiment, which maintained that drive stimulus discrimination training should reduce the amount of secondary reinforcement generalized from one drive state to another. In terms of the conditions of the four groups it was predicted that the discrimination-trained group tested under food deprivation would emit more responses than the nontrained food-deprived group, and that the discrimination-trained group tested under water deprivation would make fewer responses than the nontrained water-deprived group. Although a tendency was noted for the discrimination-trained hunger group to respond more than the nontrained hunger group, the difference was not reliable, and the first prediction must be considered to be unverified. In the case of the second prediction the difference between the trained and nontrained thirst groups ($p = .01$) was in the opposite direction from that which was predicted.

Thus, discrimination training appears to have enhanced the number of responses made by both food- and water-deprived *S*s during the 1-hr. extinction test. A possible explanation of this effect may be that the 24 days of food and water deprivation to which these animals had been subjected during the discrimination training served to increase their total effective drive level during the extinction test. Especially, it is likely that a residual hunger drive had been built up, thus accounting for the greater number of responses on the part of the trained thirst group as well as the trained hunger group.

The findings seem to offer direct evidence that secondary reinforcement, when measured as the number of responses occurring during extinction, does not generalize from one drive to another. The differences between discrimination-trained and nontrained hunger and thirst groups are significant beyond the .01 level. If the results of this and the Estes study are accepted, it seems quite possible that the sets of operations defining secondary reinforcement yield quite different phenomena. Such a possibility will be considered in more detail in the discussion of the second experiment.

In order to equate the conditions of deprivation preceding extinction and to compare the effect of presence and absence of the auditory stimulus during extinction a second study was designed.

EXPERIMENT II

Method

Subjects. Eight male and eight female albino rats of the Wistar strain, 90 to 110 days old, were used as *S*s.

Apparatus. The apparatus for this experiment consisted of the modified Skinner box previously described under Experiment I. The only further modification involved the use of a switch which prevented the food-release solenoid from being activated by depression of the bar, but continued to activate the counter which recorded bar-pressing responses.

Deprivation schedule. Prior to the administration of training in the secondary reinforcement situation, all *S*s were subjected to a replication of the 24-day schedule of alternating 22-hr. food or water deprivations which accompanied the discrimination training in the previous study, but in this experiment no discrimination training was given.

Secondary reinforcement training. All *S*s received the same schedule of training in this phase as in Experiment I; i.e., they received over a period of three days a total of 60 food reinforcements accompanied by auditory clicks following bar-pressing responses.

Extinction test. Essentially the same procedure as that in Experiment I was followed. The animals were deprived of either food or water for 22 hr. prior to the 1-hr. extinction test. In this case, however, the sound of the solenoid did not accompany the responses for one-half the *S*s of both the food- and water-deprived groups. For the remaining hungry and thirsty *S*s, the sound of the solenoid accompanied each response.

Results

Table 3 shows the mean number of times the four groups responded during the 1-hr. extinction test. The hunger group receiving the click after each response gave a mean of 317, the largest of any of the groups. There is little difference between the number of responses obtained for the two water-deprived groups, the one not receiving the click actually being

TABLE 3

Means and Standard Deviations of Number of Responses during One-Hour Extinction Period

GROUP	MEAN	*SD*
Food-deprived		
I. Click	317.0	254.1
II. No click	188.0	168.1
Water-deprived		
III. Click	28.0	42.1
IV. No click	30.0	21.9

TABLE 4

Analysis of Variance of Log Number of Responses for the Various Groups during One-Hour Extinction Period

SOURCE	*df*	MEAN SQUARE	*F*	*p*
Secondary reinforcement (click-no click)	1	0.0210		
Drive state	1	3.4567	58.68	<.01
R × D	1	0.1204	2.04	
Within set	12	0.0589		
Total	15			

slightly higher. In terms of the generalization of secondary reinforcement it would be predicted that the thirst group hearing the click should have responded a greater number of times.

Table 4 presents a summary of the analysis of variance carried out on the log transformations of the raw scores for the four groups. It is seen that a difference in drive state during extinction is the only treatment that results in a significant *F* score. When *t* tests were applied, again only those differences between hunger and thirst groups were significant. Larger groups might well have provided a significant difference between the hunger-reinforced and hunger-nonreinforced groups (the difference was at about the .10 level), but as was pointed out above, the difference between the two thirst groups, though not significant, was in the opposite direction from that which would have been predicted by a generalization hypothesis.

It should be noted that the mean number of responses for the secondary reinforced hunger group during its extinction was almost identical with the discrimination-trained hunger group of the first study. This would seem to support the hypothesis that a residual drive had been carried into the extinction period by the discrimination-trained animals of the first study.

Discussion

From the foregoing results it is apparent, as was the case in Experiment I, that number of responses that occurred during extinction provides no evidence that any secondary reinforcing effect of the click generalized from the hunger drive to thirst drive. It appears, rather, that the presence of the hunger or thirst drive stimuli during extinction was the important determiner of the number of responses emitted.

It seems possible to conclude that the effects of secondary reinforcement either do not generalize from one drive to another or that such effects operate differentially under the two sets of conditions which have defined secondary reinforcement. That the second possibility is the more likely is evidenced by the inability to date of investigators to differentiate between secondary reinforcement of the type under investigation in the present study and discrimination learning (3, 10, 11). It is suggested that when an instrumental response chain is undergoing extinction, those stimuli which were associated with the reinforcement of that chain tend to function as discriminative rather than reinforcing stimuli. This certainly is indicated by the behavior of the two thirst groups during the extinction stage of Experiment II.

SUMMARY

1. It was hypothesized that the reported generalization of secondary reinforcement from one drive state to another resulted from the animal's failure to discriminate between the stimuli associated with the two drives.

2. Twelve albino rats were trained in the typical Hull-Leeper fashion to discriminate the drive stimuli of hunger from the drive stimuli of thirst. They were then trained with 12 other animals under 22-hr. food deprivation to make a bar-pressing response to an auditory click (secondary reinforcement) and food reward. One half of each of the discrimination-trained and nontrained groups was continued on 22-hr. food deprivation, while the other *S*s were transferred to 22-hr. water deprivation. The four groups were then extinguished for a 1-hr. period with primary reinforcement absent but with the auditory click following each response.

3. The results indicate a pronounced tendency for both discrimination-trained groups to respond more during the hour than their respective nontrained groups, but fail to support the contention that secondary reinforcement has generalized from hunger to thirst under either condition.

4. A second study was designed to test the possibility that the extended period of dep-

rivation of the discrimination-trained animals preceding extinction brought about the obtained differences, and to compare the effect of the presence and absence of the auditory click during extinction.

5. Sixteen albino rats were carried through the same deprivation cycle as the discrimination-trained *S*s of the previous study, but were not given the training. Following acquisition of the bar-pressing response to the auditory click and food reinforcement, half the animals were continued under food deprivation and half changed to water deprivation. Half of each of these groups was then extinguished for 1 hr. with the auditory click present and the others without it.

6. Again there was no evidence for the generalization of secondary reinforcement. Possible interpretations of the results in terms of the relationship between secondary reinforcing stimuli and discriminative stimuli are discussed.

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Received December 3, 1953.

GENERALIZATION OF SECONDARY REINFORCEMENT IN DISCRIMINATION LEARNING[1]

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In a recent paper (4), evidence was presented showing that the learning of a black-white discrimination with rats was differentially affected by the presence or absence of an empty food cup in the negative goal box. It was argued that since the cup had acquired secondary reinforcing properties, its presence in the negative goal box would provide some reward, thus vitiating somewhat the full effects of nonreinforcement and thereby retarding the development of a differential response.

If the principle of stimulus generalization applies to secondary reinforcing stimuli, it follows that the rate of learning a visual discrimination will be affected by the amount of habit strength that generalizes from the secondary reinforcing cues on the rewarded stimulus to those on the nonrewarded stimulus. For example, if the food cup on the rewarded stimulus is used as a secondary reinforcing agent, the presence of a *similar* food cup on the nonrewarded stimulus (high generalization) should retard learning as compared with a situation in which a *dissimilar* food cup is present on the nonrewarded side (low generalization). Essentially the same line of reasoning was used by Denny (2) in a recent experiment in spatial discrimination employing a T maze. A distinctive goal box was used as the secondary reinforcer. When identical goal boxes were present at both ends of the maze, learning was retarded in comparison with that of a group which, upon making an error, entered a box different from the one on the rewarded side.

The present paper presents the results of three experiments designed to test the effects of generalization of secondary reinforcement in a visual discrimination situation. The first study, carried out in the Iowa laboratory, confirmed the prediction. A repetition at the State College of Washington laboratory, however, failed to show a difference between the groups. The third experiment was, therefore, conducted, also in the State College of Washington laboratory, in an attempt to reconcile the discrepancy between the first two studies. The general design for all three experiments was the same. For all animals the color of the food cup on the rewarded side was identical to the color of the rewarded stimulus, i.e., black or white. The groups differed in terms of the color of the food cup on the nonrewarded side. In the high generalization group (HG), the color of the food cup on the nonrewarded side was the *same* as that on the rewarded side. In the low generalization group (LG), the color of the food cup on the nonrewarded side was the *opposite* of that on the rewarded side. According to the analysis made above, the LG group should learn the black-white discrimination significantly faster than the HG group.

EXPERIMENT I

Method

Subjects. This study was conducted in the Iowa laboratory. The *S*s were ten hooded rats, five in each group, from the colony maintained by the psychology department. These animals had previously been used in a T-maze spatial discrimination experiment and consequently exhibited strong position habits at the start of the discrimination training.

Apparatus. The apparatus (Fig. 1) consisted of a Y maze, the stem of which was walled and covered with hardware cloth. The arms of the Y were open as in an elevated maze. The entire floor and the walls of the stem were of unpainted wood. The stimuli were two 4- by 10-in. pieces of Masonite painted flat black and flat white, respectively.

The food cups (3-in. glass furniture coasters) were placed below the level of each stimulus board out of the line of sight from the choice point so that an animal had to reach down in order to obtain the pellet of food. A T-shaped door at the choice point prevented both retracing and correction.

Procedure. After one week of being fed 8 gm. per day in individual feeding cages at the experimental hour, *S*s were given four days of preliminary training to habituate them to the apparatus. During this

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[1] The major portion of a paper read at the Eugene, Oregon, meetings of the Western Psychological Association, 1949. Those data collected at the State College of Washington were supported in part by the State College of Washington Research Fund.

TABLE 1

Data from Three Experiments for High (HG) and Low (LG) Generalized Secondary Reinforcement to the Negative Cue in Black-White Discrimination

EXPERIMENT	GROUP	TRIAL			ERRORS		
		M	σ_M	p*	M	σ_M	p*
Iowa	HG	40.20	5.62	.05	20.40	3.87	.05
	LG	22.80	1.96		9.80	1.59	
1st WSC	HG	21.90	3.19		9.50	1.36	
	LG	27.20	2.93		13.10	1.51	
2nd WSC	HG	57.33	6.11	.01	26.00	2.54	.01
	LG	31.58	3.23		14.33	1.77	

* Due to heterogeneity of variance, the p values were obtained by entering the t table with $n - 1$ degrees of freedom (cf. 3, ch. 9).

period clear glass food cups were used. Following this period, the black and white cues and the appropriate colored food cups were placed on the apparatus. All *S*s were given ten noncorrection trials per day until they reached a criterion of 90 per cent correct on two consecutive days with the last ten runs all correct. During training, the position of the stimulus cues was reversed in a balanced random order.

Results

The results are presented graphically in Figure 2 as the two solid lines. The superiority of the LG group is also reflected in the mean trial and error scores, as shown in Table 1.

Even though these data support the prediction, the size of the groups, only five *S*s each, and the fact that they had previously been trained in a similar type of apparatus prompted a repetition of the experiment.

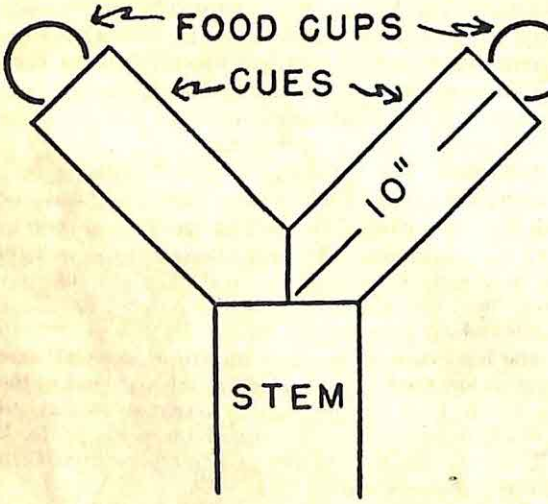

FIG. 1. Outline of the essential features of the apparatus in Experiment I. Food cups were placed below the floor level, out of line of sight from the choice point.

EXPERIMENT II

The second study was conducted in the State College of Washington laboratory. The apparatus was changed slightly, the main differences being in the floor, which was a grill, and the shape of the maze, a T instead of a Y. There were ten naive male albinos to a group. The two groups were treated the same as their counterparts in the first experiment. The results, however, were quite different, there being no significant differences between the groups (Table 1).

DISCUSSION

The problem now remains to analyze the similarities and differences in the two experiments. It is conceivable that such factors as hooded vs. albinos, degree of sophistication per se, changed apparatus, etc. might contribute to the lack of agreement between the two sets of data. Such an analysis, however, seems to indicate that an important difference might lie in the fact that in the first experiment, *all S*s had definite position tendencies at the start of their training in the discrimination apparatus. This tendency, it will be recalled, was acquired during their training in a previous T-maze experiment. In the second experiment, the *S*s were naive and only 40 per cent showed a position preference. This aspect of *S*'s behavior has important implications for our present problem in terms of the role of position preferences in discrimination theory (3). According to the theory, the differential response depends upon the development of a certain difference in the tendencies to approach the positive and negative cues. When this difference is great enough to overcome other differences such as arise from position tendencies which may be allied now with one cue, then with the other, learning is manifested.

Position preference differences thus comprise one set of factors determining the size of the differences between the approach tendencies of the stimulus cues that is necessary for manifest learning. The stronger the position preference (i.e., the greater the difference in right-left tendencies), the slower is the development of a consistent choice of the rewarded cue in visual discrimination. This prediction is easily tested.

The implications of this for the present study are indicated by the fact that out of the eight *S*s of Experiment II which exhibited strong position preferences, five were in the low generalization group, the group which was predicted to exhibit faster learning. As a subgroup, these five *S*s required more trials and committed more errors than the other five *S*s of the LG group. The difference between their mean trial scores was significant at the .05 level, that between mean error scores at the .10 level. As a more adequate check, two fresh groups of ten *S*s each were trained in a black-white discrimination. During 20 preliminary trials (employing neutral cues), one of these groups was induced to adopt a position habit. This group was significantly retarded (.02 level) in terms of both trial and error scores in comparison with the second group, which had also received 20 preliminary trials but in a random order.

Since, in a situation such as this, the reinforcing value of a neutral cue must be acquired during the course of learning, it is probably necessary to insure continued commerce with the cue *before S* reaches the criterion, if the cue is to be effective in reinforcing wrong responses. Position tendencies apparently provide such insurance. As a direct test of this reasoning a third experiment was conducted.

EXPERIMENT III

Method

The physical setting and apparatus were as in Experiment II. In this experiment, however, all animals were first induced to adopt a position habit before the black and white cues were placed on the apparatus. Otherwise, the preliminary training was the same as above. Two groups of 12 naive male albinos were used. After having responded in a free-choice situation for 20 consecutive trials to their preferred side, *S*s were given the same training as in the first two experiments.

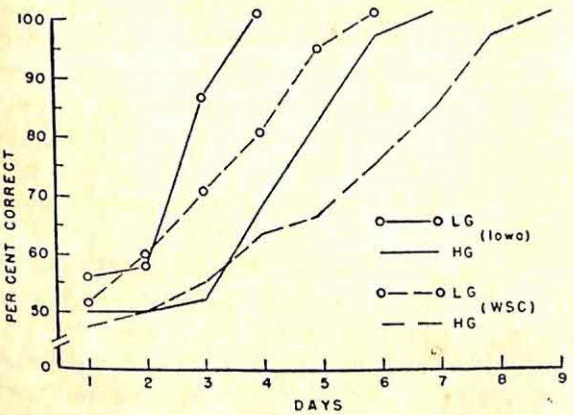

FIG. 2. Comparison curves from two similar discrimination studies showing the retarding influence of high generalization (HG) of a secondary reinforcer on the nonreinforced choice as compared with the influence of low generalization (LG)

Results

The results are also presented graphically in Figure 2 as the two broken lines. Differences between either trial or error scores are significant beyond the .01 level, in the direction predicted. Table 1 summarizes the data from all three studies.

Discussion

It thus appears that in a visual discrimination problem in which *the reward value of neutral stimuli is acquired during the course of learning*, these secondary reinforcers show the effects of generalization. Such effects are indicated by retarded learning in the group for which these stimuli are similar for both correct and incorrect choices as compared with the group for which these stimuli are dissimilar. In the present situation, the manifestation of differential generalization depended upon some such device as strong position habits for all *S*s, thus insuring enough continued contact with the secondary reinforcer on the negative choice for it to be differentially effective.

The acquisition of secondary reinforcing properties during learning is emphasized in the above paragraph since it is quite possible that had these properties been acquired prior to learning, generalization effects would have been revealed without first inducing position preferences.

There are, of course, other possibilities for "insuring enough continued contact with the secondary reinforcer on the negative choice." One is to increase the difficulty of the problem by delaying the reward. Another is to have a separate goal box which surrounds the *S*, rather than a small cup to which *S* is exposed for relatively mild periods. Both conditions were employed simultaneously in a recent study by Bauer and Lawrence (1). Their groups I and III correspond to our LG and HG groups, respectively. As in the present study, their group I learned faster than group III.

SUMMARY

Generalization of secondary reinforcement as it affects black-white discrimination learning was investigated in three similarly designed studies. In each, the generalized stimulus was the color of the food cup on the nonrewarded choice, which was either the same as or the opposite of the color of the food cup on the rewarded choice. The former arrangement is referred to as high generalization, the latter as low generalization. The hypothesis that such learning will be retarded when secondary cues occurring after a wrong choice are similar rather than dissimilar to those cues occurring after a correct choice was confirmed in the first but not in the second study. The notion that this discrepancy occurred largely as a function of the presence of strong position preference in the first study was subjected to further test. The third study, in which all *S*s were induced to adopt strong position habits prior to learning, again confirmed the hypothesis.

The role of position habits and the conditions under which they are or are not necessary in revealing the effects of differential generalization of secondary reinforcement were discussed.

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Received October 20, 1953.

EXTINCTION CHANGES DURING A SERIES OF REINFORCEMENT-EXTINCTION SESSIONS

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When a series of similar problems is learned, there is a gradual and orderly increase in learning efficiency called interproblem transfer (2, 4). Similar results (1, 5) are obtained in a repeated series of habit reversals. After the first reversal there is a sharp increase in the number of trials required to reach the learning criterion. As successive reversals are presented, there is a gradual decrease in the number of trials required to learn each reversal until learning is even more efficient than the initial attempt prior to the first reversal.

The continuous development of interproblem transfer can be readily handled by the concepts employed by Hull (3) and Spence (6), but the fact of increasing learning efficiency during habit reversals appears to present more difficulties.

This problem is specifically discussed by Hull in his latest book (3). In his reasoning it becomes a discrimination problem solved on the basis of trace from the previous responses. He concludes that such differences are difficult for nonverbal animals and it is no wonder that reversals take so long to learn.

Another attempt to explain reversal learning within the Hullian framework was made by North (5). He suggests that the advanced habit strength increment is a decreasing function of the difference between habit strength and its inhibitory components. These inhibitory effects are cumulative; consequently, the relative difference between habit strength and inhibition is reduced and large increments in habit strength can then appear. He mentions two alternatives in order to account for the continued improvement in the ability to reverse: (*a*) the relevant cues become more discriminable with practice; (*b*) there is a higher acquisition rate of either the inhibitory or the excitatory process.

Gatling (1) feels that this theory fails to account for the rather abrupt reversal shifts. According to him reversal learning is a combination of three problems: the initial problem, then learning to reverse, and, finally, shifting the response when reinforcement fails to occur. Each component would exhibit its own habit strength in reversal learning.

It appears that the development of an adequate theory must wait upon more empirical research which functions to further describe the characteristic of this kind of behavior. The purpose of this study was to investigate the extinction process during a series of reinforcement-extinctions in the Skinner box. This procedure, a constant number of reinforcements followed by extinction, was repeated again and again in a manner similar to reversal learning.

METHOD

Subjects

The *S*s were nine male albino rats 90 days old at the beginning of the experiment. They were handled daily for ten days while a feeding rhythm was established. The eating period was always 2 hr.

Procedure

Each *S* was then placed in a Skinner box, under 21-hr. food deprivation, and remained there 1 hr. or until 15 reinforcements, food pellets, were obtained. If the reinforcements were immediately attained, the *S* waited in the home cage until the hour was over and was then placed in the feeding cage. All but two of the animals conditioned within the first hour. One of these took two sessions to condition, whereas the other required three. On the next day following this initial conditioning, each *S* remained in the Skinner box for 1 hr., and no bar press was reinforced during that period. This procedure, a reinforcement followed by an extinction period the next day, was repeated 30 times. During the last five sessions the reinforcement and extinction periods did not fall on alternate days; their sequence was determined by random selection.

The animals remained in their feeding cage for 24 hr. on sessions 14 and 21, so two days elapsed between sessions. This was an accident, not a part of the experimental design. There was no noticeable change in the extinction record after these days.

RESULTS

The medium number of extinction responses made for each extinction hour is presented in

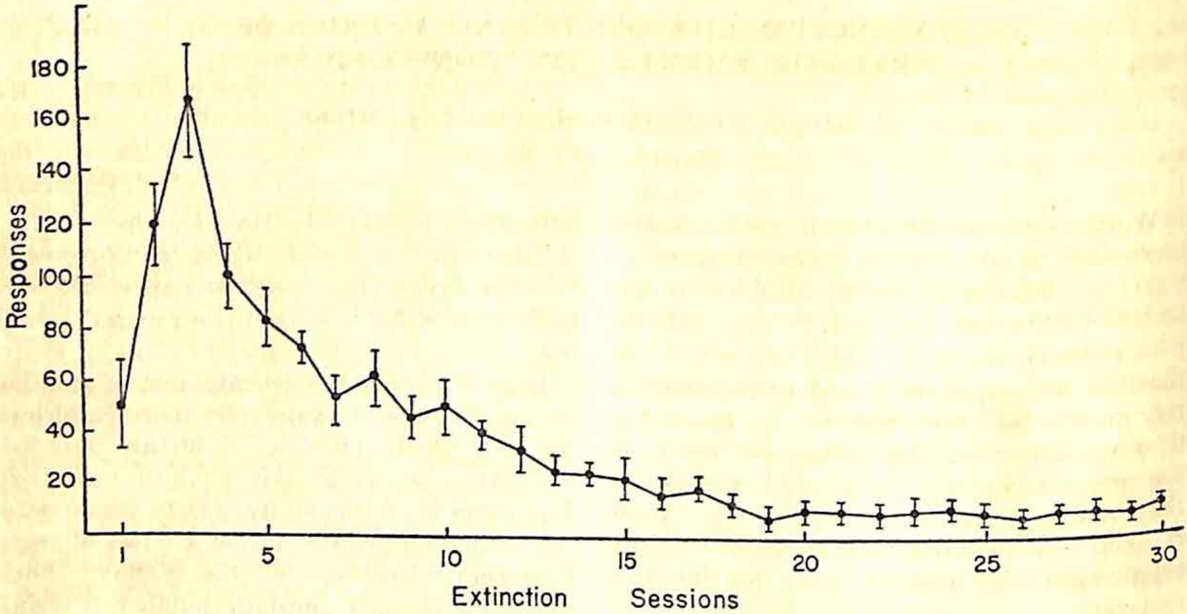

FIG. 1. Medium number of extinction responses for each extinction session

Figure 1. The vertical line at each point represents the extent of one average deviation with its center placed at the median. There is an immediate increase in the number of extinction responses, followed by a steady decrease; finally, the function maintains a relatively low and constant level.

DISCUSSION

It is felt that the pooled record of successive extinctions is representative of the individual records. All *S*s reached their maximum peak of extinction during sessions 2, 3, or 4 and maintained a high rate throughout that sequence. Also typical was the rather rapid decrease in the number of extinction responses from session 4 to 12, with the extinction record remaining fairly uniform from that point to the end of the series.

There was no change in the extinction records during the last five trials, when the occurrence of an extinction session was determined by random selection. Thus, the discrimination was not due to alternate reinforcement and extinction days, but was on the basis of a reinforced lever press.

The general form of the curve obtained in this operant conditioning situation is very similar to that of the curves obtained by North (5) on position reversal and Gatling (1) on black-white discriminations. It will perhaps be useful to analyze and compare the tasks required of *S*s in these experiments which have such similar results. In the reversal learning experiments *S*s were required to extinguish a former response and then acquire its antagonist. Changes in over-all effect could result from either of these processes, learning or extinction, or both. The present investigation indicates that changes in the rate of the extinction process follow a very similar trend. Thus, any theory dealing with habit reversal could not assume that the improvement is a result solely of superior learning of the antagonistic response.

Hull (3, pp. 114–116) uses the concept of stimulus trace to explain reversal learning in the situation employed by North, and it seems possible to utilize the same concepts in the present instance. For the animal, there is no difference in the stimulating situation on any one day until the completion of the first bar-pressing act. As a consequent of this act and the experimental arrangement, a food pellet is either received or not. Thus, when the bar is confronted on the second trial, traces of reinforcement or nonreinforcement are then present. The experimental procedure is such that on days when traces of reinforcement are present, further responses will be followed by reinforcement, but if these traces are absent, further responding is not reinforced. Hence, to solve the problem, a discrimination on the basis of traces of reinforcement or nonreinforcement must be learned.

Differential traces can be generated only after the animal has made the first response. It may be assumed that this occurs each day as a result of spontaneous recovery, if the preceding day has been an extinction day.

In the beginning of the experiment increased resistance to extinction occurred, which was followed by rapid extinction on the nonreinforced days. This successively greater increase of resistance to extinction during the early sessions could be due to a combination of initial rapid gain in $_sH_r$ of the simple bar-pressing habit and a high degree of stimulus generalization characteristic of early stages of learning.

SUMMARY

Nine male rats underwent successive conditioning and extinction of a bar-pressing habit. During conditioning 15 responses were reinforced with food pellets. On the following day the animals underwent extinction for 1 hr. This sequence of conditioning and extinction was continued for 30 sessions.

There was a sharp increase in the extinction responses followed by a definite decrease until about session 12. From that point on the number of extinction responses during each session was relatively low and constant.

The data were interpreted within a Hullian framework, using the concept of differential stimulus traces.

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Received December 10, 1953.

RESISTANCE TO EXTINCTION OF A RUNNING RESPONSE FOLLOWING PARTIAL REINFORCEMENT UNDER WIDELY SPACED TRIALS[1]

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Various studies of partial reinforcement in a runway situation have shown the superior resistance to extinction of partially reinforced as compared with continuously reinforced animals. Hull and Sheffield (4) have proposed a hypothesis to account for these results. They hypothesize that stimulation from nonreinforced trials persists in a stimulus trace for the partially reinforced animals. It becomes part of the stimulus complex on subsequent trials when the animal receives reinforcement and then becomes conditioned to the running response. Thus when extinction trials are presented, the partially reinforced animals will have had stimulus components from nonreinforced trials previously conditioned to running, while the continuously reinforced animals will not. Since the partially reinforced animals will have more of the components of the stimulus complex which occurs on an extinction trial conditioned to the response, they should prove to be more resistant to extinction.

As a test of this hypothesis Sheffield proposed that animals be given trials that are sufficiently widely spaced to permit trace stimulation from one trial to die out before the next. It would then be absent from the stimulus complex on extinction trials for the partially reinforced as well as the continuously reinforced animals. The expectation would then be that the continuously reinforced animals would be equally or more resistant to extinction, since they would have had a larger number of reinforcements than the partially reinforced animals.

The present study was run at an intertrial interval of 24 hr. and employed four values of the percentage of reinforcement variable, 100, 80, 50, and 30 per cent. Extinction was then run at a 24-hr. intertrial interval. The extinction data thus provide a test of the Hull-Sheffield hypothesis.

Further, the 24-hr. intertrial interval was chosen as that value of the variable which provided the best practical approximation to the independent sampling postulates of Estes (2) and Bush and Mosteller (1). Since spacing does not lead to such complications as changing drive levels and cumulative stimulational changes which are involved in massing of trials, the spaced-trial results should prove to be quite useful for theoretical purposes.

METHOD

Subjects

Forty-eight hooded rats, 10 females and 38 males, were used. The *S*s were 150 to 180 days old at the start of the experiment and were obtained from a local animal supply house. They had been run previously in a Skinner-box study under water deprivation.

Apparatus

The animals were run in a right-turn L-shaped enclosed runway. The width and height of the runway were both 4 in. throughout. The long arm of the L consisted of a starting box 8½ in. long, and a running alley 18 in. long. The short arm of the L was used as a goal box and was 22 in. long. The sides of the runway were made of plywood and the floor of ⅛-in. diameter brass rods spaced ½ in. apart. Sheet metal trays were placed below the runway but not in contact with it. The starting box and the running alley were painted a flat white, the goal box a flat black. The runway was covered with Plexiglas, which was hinge-mounted over the starting box and goal box to permit easy insertion and removal of the rats. Guillotine doors separated the starting box from the running alley and the running alley from the goal box. Two .01-sec. Standard Electric timers were used to obtain latency and running-time measures.

Illumination was provided by a clear 200-w. bulb suspended from the ceiling of the experimental room, approximately 1 ft. to the right and 6 ft. above the starting box. The experimental room was soundproof.

Procedure

The animals were put on their feeding schedules three days before the first day of acquisition training.

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[1] The author is greatly indebted to Professor W. K. Estes for his generous advice and encouragement throughout the course of the experiment reported here. An abbreviated version of this paper was presented at the 1953 meeting of the Midwestern Psychological Association in Chicago.

[2] Now SSRC Postdoctoral Research Training Fellow at the Laboratory of Social Relations of Harvard University.

The animals were then randomly assigned to experimental groups, 12 animals to a group.

The animals were run one trial a day under 23 hr. of food deprivation. All animals received reinforcement on the first four trials. On the next 70 days they were reinforced according to the groups to which they had been assigned. The groups received 100, 80, 50, and 30 per cent reinforcement. Each animal in the partially reinforced groups had its nonreinforced trials during acquisition assigned randomly by blocks of ten trials.

On reinforced trials the animals had a Mason jar top of wet mash available for 30 sec. from the time they entered the goal box. On the first two trials the animals were allowed to remain in the goal box until they had eaten for 5 sec. if they had not begun to eat during the first 25 sec. The jar top was placed touching the far wall of the goal box midway between the two side walls. On nonreinforced trials the jar top of wet mash was removed from the goal box and placed on a platform 2 in. to the rear of the long side of the goal box that was more remote from the starting box and ½ in. above the level of the floor of the goal box. The jar top of wet mash was also placed on the rear platform during extinction trials. On all nonreinforced trials the animals were left in the goal box for 30 sec.

The animals were run in the same order each day, one cage at a time. Just before its run, each animal was removed from the home cage and put into the starting box. Five seconds later the starting box door was raised, and the two timers were automatically started when the door was fully open. One timer was stopped by a manual switch when the animal had all paws out of the starting box, providing a latency measure, the other when the animal had all paws in the goal box, providing a running-time measure. A stop watch was started when the animal entered the goal box, and after 30 sec. the animal was removed and returned to its home cage. During the 30-sec. period the latency and running time were recorded and the apparatus and clocks reset. Twenty to 30 min. after running, the animals were fed for ½ hr. from Mason jar tops containing wet mash.

The animals were reinforced according to schedule for the first 74 days, providing 75 trials for the acquisition phase; no animal was reinforced for the last 21 days, providing 20 trials for the extinction phase. No a priori criterion for asymptote was adopted since there was no prior information concerning asymptotic behavior under the conditions of this experiment. Thus the point at which extinction was begun was arbitrary. It was chosen when the running-time and latency curves seemed, to *E*, to have leveled off.

Six animals were eliminated during acquisition and two during extinction. These eight animals were males. Of these, two animals, one in the 30 per cent group and one in the 50 per cent group, failed to meet a 15-min. criterion on the first trial and were discarded. Two animals in the 50 per cent group were discarded since they bit *E* with such tenacity that the latter's behavior in prying them loose made them useless for further experimentation. Two animals, one in the 100 per cent and one in the 80 per cent group, died of natural causes during acquisition, while two additional animals, one in the 100 per cent and one in the 50 per cent group, died of natural causes during extinction.

TABLE 1

F Values for the Acquisition Phase*

VARIABLE	ACQUISITION TRIALS 6–15	ACQUISITION TRIALS 66–75
Mean reciprocal latency	<1	<1
Mean reciprocal running time	2.12	2.31

**F*'s based on 3 and 38 *df*. $F = 2.85$ at the .05 level.

RESULTS

Acquisition

The latency and running-time measures were converted to reciprocals to satisfy the conditions of the analysis of variance. Means of the reciprocal measures were taken for each animal for trials 6 through 15 and 66 through 75, and analyses of variance were run. The results of these analyses are given in Table 1.

From Figure 1 it may be seen that the higher percentage reinforcement groups are reasonably well ordered for the first three blocks of five trials following the introduction of the experimental variable. To avoid repetition, only the mean reciprocal running times are given. The mean reciprocal latencies show approximately the same changes. These differences are not significant at the .05 level. Figure 1 also shows an irregular ordering of the experimental groups on the mean reciprocal running-time measure during the last stages of acquisition, with the differences not significant at the .05 level.

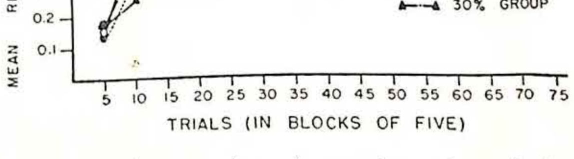

FIG. 1. Mean reciprocal running time during acquisition

TABLE 2

F Values and Bartlett Test p Values for the Extinction Phase*

VARIABLE	EXTINCTION TRIALS 1–10		EXTINCTION TRIALS 11–20		EXTINCTION TRIALS 1–20	
	F	p	F	p	F	p
Mean reciprocal latency	5.95	>0.2	8.78	>0.3	8.64	>0.8
Mean reciprocal running time	8.68	<0.05	14.60	<0.01	10.90	<0.01

* F's based on 3 and 36 df. $F = 4.38$ at the .01 level.

Extinction

Means of the reciprocal latencies and reciprocal running times were taken for each animal for the first 10, second 10, and all 20 extinction trials, and analyses of variance were run on these measures. The results of these analyses and the corresponding Bartlett tests are presented in Table 2.

From Figure 2 it may be seen that extinction proceeds in an orderly fashion with the smaller percentage reinforcement groups showing the smaller slopes. Particularly striking is the 100 per cent group, which reaches a stable, low mean reciprocal value after four extinction trials.

In Table 2 it may be seen that p values at or below the .05 value are obtained for the Bartlett test for the mean reciprocal running-time measure. Thus, it is not known whether the significant F's are to be attributed to differences between means of the groups or to the nonhomogeneous variances.

To make an appraisal of the situation, one group at a time was dropped from the analysis in the hope of satisfying Bartlett's test. Bartlett's test gave a $p > 0.3$ when the 100 per cent group was dropped from the analysis for trials 1 through 10. The resulting F was 3.45, which is significant at the .05 level.

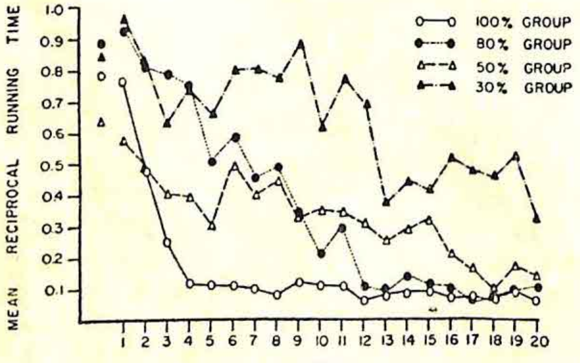

FIG. 2. Mean reciprocal running time during extinction. The initial, unconnected points are the means of the last block of five acquisition trials.

Further, a nonparametric test, Mood's median test (3), was applied to the same set of measures and yielded chi squares, with 3 df, of 16.4, 18.0, and 17.5 for the running-time measure for trials 1 to 10, 11 to 20, and 1 to 20, respectively. All these values are significant at the .01 level. Mood states that the median test is sensitive mainly to differences in central locations.

To obtain further information, an extinction index was defined as the frequency in 20 trials with which an animal gave smaller running times than twice its median running time in the last block of 10 acquisition trials. Mood's median test was then applied to these indices and yielded a chi square, with 3 df, of 14.8, which is significant at the .01 level.

In view of these considerations, the author's evaluation is that the differences obtained on the running-time measure during extinction are largely due to differences in central location.

There are two major findings: animals receiving varying percentages of reinforcement arrive at the same final level of responding, and animals receiving smaller percentages of reinforcement exhibit greater resistance to extinction.

DISCUSSION

Since the trials were widely spaced in the present study, the extinction results obtained are not accounted for by the Hull-Sheffield hypothesis. The problem of partial reinforcement, which seemed to be so neatly wrapped up by that hypothesis, must be reopened.

The following notions, cast in a contiguity theory framework, seem to the author to be able to handle the two major features of the present results. According to contiguity theory the role of the experimental operation of reinforcement is to remove the animal from stimulation. The last response made prior to the termination of the stimulation will then be conditioned. In experimental extinction reinforcement is withheld. The animal then makes other, or competing, responses which are, in turn, conditioned to the stimulation.

The result is a decrement in response strength of the original response class. So far, this is standard contiguity theory.

The author goes on to assume that the competing responses which the animal makes to an empty goal box on a nonreinforced trial habituate during the course of a series of nonreinforced trials. Thus, partially reinforced animals, which have had some number of nonreinforced trials during acquisition, will have their competing responses to an empty goal box habituated to some relatively low level. The competing responses, having habituated, will occur with a low frequency, and there will be little decrement in the strength of the original response due to the presentation of a nonreinforced trial.

The decrease in frequency of competing responses seems to be visible in the behavior of the partially reinforced animals. On early nonreinforced trials they go to the food place, find no food, and run about the goal box. On later nonreinforced trials the running-about behavior has dropped out and the animals remain in the vicinity of the food place.

Thus, for the partially reinforced animals, the running response is built up and maintained by the operation of reinforcement. Omission of reinforcement leads to the occurrence and habituation of competing responses made after the animal has run to the food place. Late in a series of reinforced and nonreinforced trials the amount of decrement due to a nonreinforcement is small. Thus, the partially reinforced animals should achieve almost the same level of responding as the continuously reinforced animals.

According to the notions presented, there should be a direct relation between percentage of reinforcement and asymptotic speed of running. The notions advanced, however, would lead us to believe that the differences in final running level of the various groups should be small. In view of the small number of animals run in the present study, the result of equal final running levels may be regarded as compatible with the notions advanced.

The development is easily extended to the extinction data. If we have a number of partial reinforcement groups each receiving the same total number of trials, there will be orderly variation in the number of nonreinforced exposures which they have had to the goal box. Thus, the lowest percentage reinforcement group will have had the greatest number of nonreinforced exposures during the acquisition phase, and the highest percentage group will have had the smallest number. We should then expect the greatest amount of habituation of competing responses to have occurred in the group having the smallest percentage of reinforcement, or the largest number of nonreinforced exposures.

Due to habituation, then, we should expect the least frequent occurrence of competing responses to the empty goal box during extinction for those animals which have had the largest number of nonreinforced trials, and the most frequent occurrence of competing responses for the group that has had the smallest number of nonreinforced trials during acquisition. That is, the smaller the percentage of reinforcement given during acquisition, the less behavior competing with the running response will occur during extinction. Application of the standard contiguity treatment of extinction then gives the desired result of increased resistance to extinction by the smaller-percentage-of-reinforcement groups.

On the other hand, the continuously reinforced group will have had no nonreinforced trials. It will have had no chance to habituate its competing responses, and they will be at their highest strength. Thus, the continuously reinforced group will show the greatest decrement in the strength of the running response during extinction.

As a result, one would expect the orderly extinction results which were actually obtained. The notions developed handle both major features of the experimental results.

SUMMARY

Forty-eight hooded rats were given acquisition and extinction of a runway response at a 24-hr. intertrial interval under 23 hr. of food deprivation. Four groups received 100, 80, 50, and 30 per cent random reinforcement during a 75-day acquisition series. Then all groups received a 20-day extinction series.

For the last ten days of acquisition there were no significant group differences in latency and running time.

During extinction group differences were significant beyond the .01 level, with an inverse relationship between percentage of reinforcement and resistance to extinction.

In view of the large intertrial interval, the extinction results cannot be handled by the Hull-Sheffield hypothesis. A modified contiguity theory was proposed to handle these results. It remains possible that both theories may be useful in dealing with massed-trial experiments.

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Received October 15, 1953.

RESPONSE STRENGTH AS A FUNCTION OF REDUCTION IN RATE OF SUBGOAL REINFORCEMENT

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The present article reports evidence concerning the energizing effect of an increase in the accustomed time interval required to secure marble subgoals in an ordered instrumental sequence.

Though not yet well established, the indication is that interference of goal-directed activity (delay, nonreward, blocking, etc.) results in some cases in energizing ongoing behavior, that is, in increasing its amplitude or rate (2, 4, 5). This energizing effect of interference frequently is regarded as having "emotional" or motivational significance, though nonemotional interpretations of the effects of interference, given present evidence, are also possible (1). Apart from the theoretical possibilities, the more immediate problem seems to be the more precise delineation of those relevant stimulus properties of interference which relate to energizing effects.

The present experiment is based on the possibility that the change in the accustomed temporal order of events introduced by most interference situations may be an important stimulus property affecting response strength. Goal-directed activity in which energizing effects have been noted usually involves a familiar situation comprising an ordered series of *previously learned* steps which, after learning, take a more or less constant amount of time to perform. One might hypothesize that the basic difference between ordinary problem solving in its early stages and so-called "frustration situations" is this disruption of an established temporal sequence in the latter case. As an initial test of this hypothesis, two groups of children were accustomed to an instrumental sequence which differed only in terms of the amount of time required to complete the sequence. The accustomed time interval between subgoal reinforcements of the faster group was then increased to that of the slower group and a comparison made of the amplitude of the ongoing behavior of the two groups.

METHOD

Subjects

A total of 23 kindergarten children, 58 to 80 months of age, were used as *S*s in the present experiment. All *S*s were taken from the YW-YMCA–supervised kindergarten at the University of Mississippi. There was a total of 12 male and 11 female *S*s in the sample.

Apparatus

The apparatus, similar to that used in an earlier experiment on interference (4), consisted of a large box on the face of which was a crank, a vertical panel of jeweled lights, and a marble dispenser. Turning the crank operated a relay which activated the succeeding events. A counter relay lit each panel light, one at a time, proceeding from the top of the panel downward. At the bottom light, a solenoid dispensed a marble into a cup. Activation of the counter (and panel light movement) was controlled by a Hunter Interval Timer, which could be set at any desired interval. Movement of the panel lights was thus independent of the rate of crank turning.

The crank was connected to a small 10-v. generator, which was fed into the sweep pen of an Esterline-Angus recording voltmeter. Changes in speed of crank turning resulted in changes in voltage output, which was then graphically recorded on scaled polygraph paper. This change in voltage output thus served as the quantitative measure of response strength (speed of crank turning) in the present experiment. Future references to the rate or speed of crank turning are thus voltage measurements. Because of the nature of the recording device, the most practicable method proved to be the highest rate reached over the period of time represented by each trial. This is a departure from the measure of crank turning used in the earlier studies of Screven (4) and Howell (3), where mean number of turns per trial was plotted as a function of the experimental variables.

Procedure

The *S*s were assigned at random to two independent groups, an experimental and control, with *N*'s of 11 and 12, respectively. Sex distributions were approximately equal. Each *S* completed two sessions administered on separate days.

Session I. All *S*s were required to turn the crank for a total of 15 trials on each of which the panel lights moved downward through ten positions and a marble was received and placed in a box at the left of the crank apparatus. The *S*s were required to turn the crank continuously throughout each panel sequence, which defined each trial. An approximately constant between-

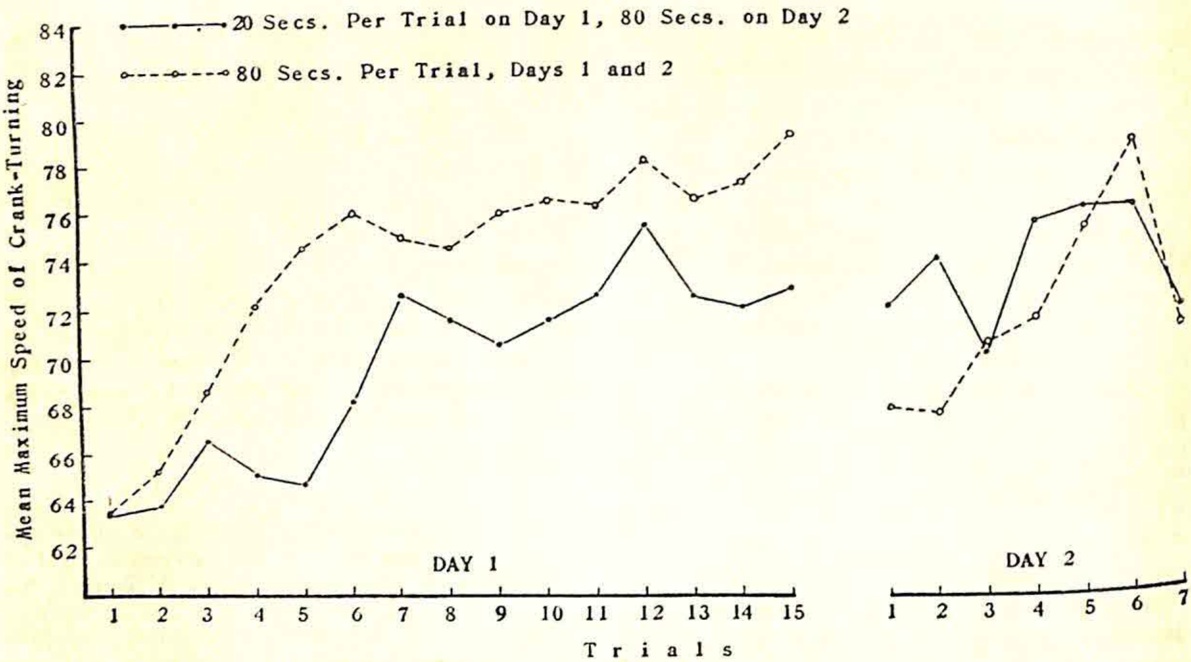

FIG. 1. The effect of reduction in rate of subgoal reinforcement on maximum speed of crank turning

trials interval of 30 sec. was maintained by requiring *S* to wait for the sound of a buzzer before beginning the next trial. No instructions concerning speed were given. Each *S* was told that when he had put enough marbles in the box, a bell would ring, entitling him to choose any one of three drawers and keep the prize he found. There was a prize in each drawer.

Experimental and control groups differed on Session I in terms of the time required for each successive downward movement of the panel light and thus the time required to obtain the marble subgoals. For experimental *S*s the panel lights moved downward every 2 sec., taking a total of 20 sec. to complete the panel and receive a marble. For control *S*s, the panel lights moved downward every 8 sec., taking a total of 80 sec. to receive each marble. After *S*s in both groups received a total of 15 marbles, the bell rang and *S*s were allowed to choose one of the drawers, take their prize, and return to the kindergarten.

Session II. The second and final session followed in from one to three days. The procedure was the same as in Session I except that the duration of each trial was now 80 sec. for *both* groups (8 sec. per panel light). Thus, Session II involved no change for control *S*s but involved an increase for experimental *S*s from 20 sec. to 80 sec. required to complete the panel and receive a marble. Only seven trials were administered during Session II, after which a prize was received as before and *S*s returned to the kindergarten.

RESULTS AND DISCUSSION

Figure 1 shows the mean highest rate reached per trial on Sessions I and II for the two groups.

Of primary interest are the differences between the change and no-change groups at the beginning of Session II. The experimental group, for whom trial durations were now 80 sec., as compared with 20 sec. on the previous session, was superior in mean maximum speed for the first two trials. This mean maximum speed was similar to the final level of the previous session. The maximum speed of the control group *S*s, who experienced no change from Session I, exhibited a marked drop from the final level of the previous session. A comparison of the two groups in terms of the final two Session I trials and the first two Session II trials yielded a mean increase of 1.92 for the experimental group and a mean drop of 10.68 for the no-change group, the total difference in change from Session I to II being 12.60 points. A difference this large would occur by chance less than 1 in 100 times ($t = 3.09$, $df = 21$). The initially lower speed of turning and "warm-up" period exhibited by the no-change group at the beginning of Session II is consistent with earlier pilot studies involving separations of a day or more between sessions. From Figure 1 it is also evident that the initial differences between the groups disappeared with continued trials under the 80-sec. condition.

In accordance with original expectations, these results suggest that the increase in the accustomed trial duration did temporarily energize ongoing response strength as measured by maximum speed of crank turning. Since maximum speed of turning per trial was the only measure used, the present results do not indicate whether this effect was a gross increase in over-all rate of turning or a sporadic effect leading only to occasional bursts of greater strength.

In Figure 1, control *S*s turned at a higher maximum speed during Session I than experimental *S*s. However, statistical analysis revealed that these apparent differences between the two groups were not greater than chance expectation.

SUMMARY

Two groups of kindergarten children were accustomed to an instrumental sequence involving the continuous turning of a crank for marble tokens which could be exchanged for a prize (Session I). The two groups differed as to the amount of time required to complete each sequence and receive a marble. On Session II (a different day), the accustomed time of the faster group (20 sec. per marble) was increased to that of the slower group (80 sec. per marble), who experienced no change. The mean maximum turning speed for the final two trials of Session I was compared with the first two trials of Session II.

The no-change group showed a marked drop in speed from the final maximum speed of the previous session followed by a gradual "warm-up" to the level of the previous session. The change group showed no such drop in maximum speed. A difference as large as the one obtained between the two groups would occur by chance less than 1 in 100 times. This result was interpreted as suggesting an energizing effect of change in accustomed rate of subgoal reinforcement.

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Received October 16, 1953.

EFFECT OF EARLY SOCIAL EXPERIENCE ON ADULT AGGRESSIVE BEHAVIOR IN C57BL/10 MICE[1]

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Variations in the early physical and social experience of young animals may have immediate effects on the young, later effects upon mature animals, or both. Although this is not a surprising fact, it is the aim of many investigators to ascertain the specific kind of early experience that affects a particular adult pattern of behavior. For example, Griffiths and Stringer (5) found that intense stimulation (shock, cold, noise, etc.) administered to rats during their first 21 days of life had no effect on maze learning and emotionality at maturity. Bingham and Griffiths (2) found that variations in the physical environment of young rats did influence their adult performance in the Warner-Warden maze. Similar investigations have been made to evaluate the effect of early social experience. Ross (9) found that puppies deprived of their mother tended to exhibit excessive nonnutritional sucking. Beach (1) reported that male rats raised in isolation were more active sexually than males raised with females or with other males. Scott (10) observed that lambs isolated from the flock never became thoroughly integrated into it as adults. Kahn (7) found that male mice raised in isolation from weaning were more aggressive than males raised with their mothers. Fredericson (4) found that mice taught to compete for food before 35 days of age fought over food when 72 days old, whereas controls without the early competitive training did not fight. Although the physical variables, such as shock treatment and standard rearing cages, in the early environment of young animals have been rigidly controlled and precise physical tests have been used to measure their adult behavior, these are frequently more difficult for studying the effects of early social experience. One aim of this study was to control carefully the early social experience of mice, and later to subject the animals to a precise social test.

The early social experience that was varied in this study was association with siblings, because we believed this would influence their aggressive behavior as adults. Aggressive behavior is defined here as the readiness to initiate a vigorous fight. Animals raised in a group probably compete occasionally for food, water, and space. Although this competition may not be expressed in overt aggression, the early competitive training should make them more ready to fight than animals raised in isolation and lacking this competitive training. This attempt to explain the possible effects of early experience on adult aggressive behavior has little in common with the suggestion that early isolation and maternal deprivation create frustration leading to aggression (7). The amount of competitive training an animal receives in its early life could vary, depending upon the nature of the group with which it associates. Since males are more aggressive toward other males than they are toward females (11), males raised with females should have less opportunity to learn aggressiveness than males raised with males.

The purpose of this paper, then, is to test the general idea that an animal's early social experiences significantly affect his social behavior as an adult. The two specific hypotheses adopted were: (*a*) that male mice raised together show more aggressive behavior when mature than those raised alone, and (*b*) that male mice raised with females show less aggressive behavior when mature than males raised with other males.

METHOD

Subjects

The mice used in this study were C57BL/10 males. A total of 70 males was used, divided into three groups.

Group I. Twenty-four males were isolated at 20 days

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[1] This investigation was done while the senior author was a Postdoctoral Research Fellow of the National Institute of Mental Health and was also supported in part by research grant MH123 from the National Institute of Mental Health of the National Institutes of Health, Public Health Service.

[2] The authors wish to thank the following investigators at the Division of Behavior Studies of the R. B. Jackson Memorial Laboratory for critically reading the manuscript: J. P. Scott, J. L. Fuller, F. J. Bauer, and W. R. Thompson.

of age and raised without any contact with other animals until placed in the testing situation at 107 to 112 days of age.

Group M. Thirty-four males were separated from their mothers and all female siblings at 20 days of age and raised with only their fathers and male siblings until 45 days of age, at which time they were isolated until placed in the test situation at 105 to 115 days of age.

Group F. Twelve males were separated from their mothers, fathers, and all male siblings at 20 days of age and raised with only their female siblings until 45 days of age, at which time they were isolated until placed in the test situation at 107 to 114 days of age.

None of the individuals in the three groups had contact with its mother after 20 days of age. Thus, any effects of weaning and nutrition from the mother were eliminated. The fathers were left with group M mice in order to increase the number of male associations of the experimental mice. It is possible that the fathers are more antagonistic toward their offspring than the littermates are among themselves. If the young were attacked by a superior fighter, such as their father, they should learn to be defensive and to inhibit fighting responses. However, it is unlikely that serious conflicts develop between father and offspring before 45 days of age.

Since the number of young varies from litter to litter, the males raised with males (group M) were exposed to the father and at least one other sibling and not more than five other siblings. Males raised with females (group F) associated with two to five female siblings. During the tests, the animals were not paired with any reference to the number of animals with which they were raised. It is possible that the number of animals raised together has some effect on their later behavior; however, this uncontrolled variable could not affect the hypotheses.

Apparatus

The mice were fought in boxes similar to those in which they were raised, except that the partition separating the two 12-in. by 6-in. by 6-in. living cages was removed, thus doubling the size during each trial.

Procedure

Three days before being tested the mice within each group were paired with other members of their group in the fighting boxes. Only one pair in group M consisted of siblings; other pairs were composed of total strangers. For a period of ten consecutive days, individuals of each pair were exposed to each other for a maximum of 5 min. each day by removing the partition which separated them. The principal measure of aggressive behavior used in this experiment was the fighting response latency (3), which is taken as the elapsed time from the moment when the partition was removed until the first vigorous fight began. As soon as the pair fought 5 sec., they were separated by replacing the partition. This was done to prevent the development of dominance. After each pair had ten trials, individuals of one group were paired with individuals of another group. These mixed pairs were allowed to fight until one became dominant over the other. We believed that this test of dominance afforded an additional measure of aggressive behavior, although the mice were no longer naive to the experimental situation.

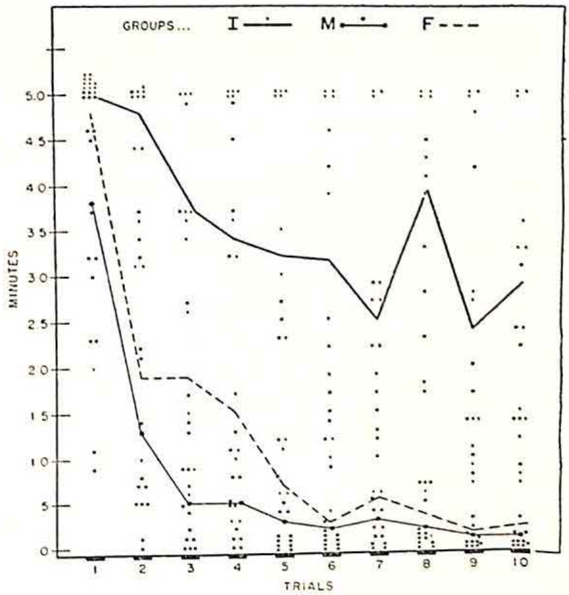

FIG. 1. Scatter diagram of fighting response latencies for groups I and M, with curves of the median response latencies for groups I, M, and F

RESULTS

A scatter diagram showing the response latency during ten trials for each pair in groups I and M and a curve showing the median score for groups I, M, and F are shown in Figure 1. It can be seen from this diagram that the distribution is not normal; instead, the highest concentrations of latencies are at the 5-min. and below the 0.5-min. level. The median illustrates the differences between the groups better than the mean, and a nonparametric test (8) was employed to ascertain the differences between the groups. In contrasting groups I and M, each trial showed that group I mice are significantly ($p = .01$) slower to fight than group M mice except for the fourth trial, in which the difference between the two groups was at the .05 level of probability. When all the trials of each pair were combined, the aggressive behavior as measured by the fighting response latency of group M was significantly ($p = .001$) greater than that of group I.

The small number of pairs ($N = 6$) in group F does not permit such rigid conclusions. However, group F animals were significantly more ready to fight ($p = .007$) than group I animals, but not significantly different ($p = .26$) from group M animals. Although the differences between groups M and F are not significant, in each of the ten trials group F animals tended to be slower to enter combat than group M animals. Study of additional pairs may indicate a significant difference between groups M and F.

The slope of the curve suggests that the mice learned to fight; those in groups M and F learned to fight much more rapidly than those in group I. Two pairs in group I failed to fight during any of the ten 5-min. trials, and two others fought only twice. Group I mice fought only 14 trials out of 120 (12 per cent) in less than a minute, while group M mice fought 109 trials out of 170 (64 per cent) in less than a minute. Frequently, after the first combat, group M mice would leap at each other and immediately begin a vicious fight in succeeding trials. In contrast, group I mice usually nosed and groomed each other for several minutes before they worked themselves into a fight. Only in the last four pairs of group I mice tested was there a tendency to behave like the group M mice during the test. The difference between group I mice tested earlier and the last four pairs tested may have been the result of noisy construction going on inside the laboratory. It is possible that the noise upset the mice and made them more irritable.

When group I and M mice were paired and allowed to fight until dominance was established, group M mice won 17 out of 23 encounters (74 per cent), which again suggests that group M mice were more aggressive than group I mice. Since it is possible that some of the mice established dominance in some of the intragroup fights, and since the mice in group M had more experience in fighting, the results of these intergroup fights are not conclusive.

DISCUSSION

The results of this experiment clearly support the hypotheses that early social associations may affect adult social behavior and that males raised with males tend to be more aggressive than males raised in isolation. However, they do not support the hypothesis that males raised with males tend to be more aggressive than males raised with females. Males raised with males and males raised with females are more like each other than either is like males raised in isolation.

Many types of early experience have a lasting effect upon the adult behavior of an animal. Some types of experiences are more important in shaping later behavior than others. For example, Hymovitch (6) found that the nature of the early perceptual environment was influential in determining later adult learning, while Griffiths and Stringer (5) found that intense stimulation during infancy did not affect adult learning. In all such experiments it is necessary to find the cause and effect relationship between the early experience and the adult behavior. Once this relationship is discovered, it is essential to learn the nature of this relationship.

In the study reported here, a relationship was found between early social associations and adult aggressive behavior. We then know that early *social* experience is important to the adult behavior in respect to aggressive tendencies. The specific hypotheses attempt to explain the nature of this relationship.

There are two explanations which may describe how the early social contacts may affect adult aggressive behavior. One explanation of this relationship is centered about the early learning of aggression and the other about the adults' reaction to the new or strange. These two explanations are not radically opposed; one stresses the learning to fight, while the other stresses only the learning to recognize another individual.

The possibility that the animals learn aggression through their early social contacts has much in its favor, but does not adequately explain all the observations. Although animals raised together in a litter rarely engage in serious fights, particularly before 45 days of age (12), there are many opportunities for competition to arise. They may push each other away from food or water, they may shove each other around while huddling together, or one may be more active in grooming or nosing another. No overt aggression may be displayed, but through the frequent competition among the members of the society a latent learning of aggression may occur. When the adult individuals are then placed in a situation which usually produces aggression, the animals which have these early competitive experiences are more ready to enter a fight than others lacking these early experiences. The curve of response latency against trials, which so closely resembles a learning curve, shows that after one trial the animals learn to perform their aggressive acts much more rapidly than those deprived of the early experiences and suggests that latent learning has occurred. This is also suggested by the similarity in the curves of group M and F animals. Males fight females only when trained, so the males raised with females probably never learned to fight, but many have competed with the females for food, water, or space.

Instead of learning competition and aggression from their early social associations, the alternative explanation suggests that the mice merely learn what another mouse is, so when confronted with another mouse for the first time, it is not entirely strange. If the mice are entirely new to each other, innate aggression is inhibited while the animals investigate each other. Although it has not been systematically tested, any new or strange situation tends to inhibit aggression. Strange boxes, removal of the cage lids, even changes in the intensity of lighting may inhibit fighting. Furthermore, the novelty of a situation may have additive effect in inhibiting the fighting response. A new box, similar to the old box, may have less inhibitory effects than a new and different type of box. In our test situation, one half of the fighting box was always new to each mouse, at least during the first trial. This new and enlarged cage and the other strange mouse seem to inhibit aggressive behavior during the first trial. However, the other mouse is not as strange to animals of groups M and F, who had lived with other mice 65 days prior to the test, as it is to group I animals, whose last contact with other mice was at weaning, 90 days prior to the test. Consequently, the group M and F animals require less exploration and getting acquainted than the group I mice. Once they become familiar with the strange mouse, aggression is no longer inhibited and fighting occurs. Group I mice take longer to investigate the strange mouse, they groom and nose him frequently, and finally, when they are no longer new to each other, they fight.

Both explanations appear to satisfy the results; however, before either is accepted or both are rejected, further tests of the relationship between early social associations and adult aggressive behavior must be made. The present experiment only permits us to conclude that such a relationship does exist.

SUMMARY

1. One general and two specific hypotheses were tested in this experiment: that an animal's early social experience affects his social behavior as an adult; and, specifically, that (*a*) male mice raised with other male mice show more aggressive behavior than males raised in isolation, and (*b*) male mice raised with males show more aggressive behavior than males raised with females.

2. Three groups of C57BL/10 mice with different early social associations were tested for adult aggressive behavior: group I—24 males raised in isolation from 20 to 107–114 days of age; group M—35 males raised with males from 20 to 45 days and then isolated until 107 to 115 days of age; and group F—12 males raised with females from 20 to 45 days and then isolated until 108 to 112 days of age.

3. When tested for adult aggressive behavior at 107 to 115 days of age by the Fredericson response latency test, group I mice were found to be significantly (p = .001) less aggressive than group M and F mice. These results support the general and the first specific hypothesis. Group M mice were not significantly different (p = .26) from group F mice, which does not support the second specific hypothesis.

4. Two explanations for the relation between early social associations and adult aggressive behavior are given. One explanation suggests that there is a latent learning of aggression through the competitive associations of mice raised in groups. This learning makes the animals raised in groups more ready to fight than those raised in isolation. The alternative explanation suggests that the innate tendency for aggressiveness is inhibited in direct proportion to the strangeness of the situation. Animals without early social associations are more strange to each other than those with early social associations and are,

therefore, more inhibited in a potential fighting situation.

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Received November 2, 1953.

THE EFFECT OF EARLY PERCEPTUAL LEARNING ON THE BEHAVIORAL ORGANIZATION OF ADULT RATS[1]

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This study was concerned with determining the effects of visual and proprioceptive experiences, during the early life of rats, on their emotional, perceptual, and problem-solving behavior at adulthood. The problem arose out of the work of Hebb and his associates (3, 4, 5, 6). Hebb has suggested that the organization of adult behavior is largely determined by the quality of infant experience and learning (4). This early learning is so important because it produces permanent changes in the structure of the central nervous system, primarily the cerebral cortex (5).

The brief history of research in this area was summarized by Hymovitch (6), who found that rats reared in a complex free environment were significantly superior in problem-solving ability, as measured by the Hebb-Williams test, to those reared in a restricted environment. The complex free environment was a large box containing a number of "playthings" (small metal and wooden structures), which enabled the rats to have a variety of experience. He also placed in this box a number of small mesh cages in which smaller groups of rats were reared. The mesh cages were periodically moved from place to place both inside and outside the box. The problem-solving behavior of these rats, as adults, was as good as that of the animals reared in the entire box. In a similar study Forgays and Forgays (3) reported, among other facts, that the rats reared in mesh cages were inferior, in problem-solving behavior, to animals reared in a large, complex free environment. Although these two sets of results are somewhat inconsistent, both authors concluded that early perceptual experience or learning seemed to play a dominant role in determining problem-solving abilities of adult rats. The importance of proprioceptive experience or learning, however, could not be clearly ascertained, since the two findings were different in this connection.

The present study was undertaken for two reasons: (*a*) to determine the relative effects of infant visual and proprioceptive experiences on the cognitive behavior of mature rats, by controlling these two infant experiences more adequately than in the previous studies; and (*b*) to ascertain the generality of the reported differences, by using criteria other than "intelligence" tests.

GENERAL DESIGN

Three groups of male hooded rats, weaned at approximately 24 days of age, were reared under different conditions[3] until they were 84 days old. Each group consisted of 14 rats.

Rearing

Group 1. These rats constituted the "complex visual-proprioceptive" group. They were reared in an environment which provided extensive opportunity for visual and proprioceptive experience. The apparatus was a large plywood box 4 ft. long, 4 ft. wide, and 16 in. high with ½-in.-grill cover and ¼-in.-grill floor. The walls were painted a flat black. A large number of white objects, such as blocks, alleys, tunnels, elevated platforms, and inclined planes, were distributed around the sides of the cage, within 13½ in. from the walls. These objects were similar to the structures previously reported (3, 6). Since these rats were permitted to *traverse* and *see* this well-articulated environment, they had much opportunity for varied proprioceptive and visual experience.

Group 2. These animals were called the "complex visual but minimum proprioceptive" group. They were reared in a box similar to that which housed group 1. However, they were only permitted to live in the inner 441 sq. in. of their cage. This was accomplished by inserting a glass cage 21 in. long, 21 in. wide, and 16 in. high inside a large box, identical to cage 1. These animals had a complex visual environment because they could see a well-articulated environment. But, since they were not permitted to traverse the objects, there was little opportunity for proprioceptive feedback from the objects they saw. It is quite clear that, relative to group 1, group 2 had minimum proprioceptive experience although their visual experience was presumably as complex.

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[1] This paper is based on a dissertation, supervised by Professor R. B. MacLeod, which was submitted to Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy and is on file in the library of Cornell University. The research was partly financed by scholarships from the Canadian National Research Council.

[2] Now at the University of Pennsylvania.

[3] Photographs of the three environments are presented in the filed dissertation, previously cited.

Group 3. This was the "minimum visual-proprioceptive" group. They were reared in a small black box 21 in. long, 21 in. wide, and 16 in. high with ½-in.–grill top and ¼-in.–grill floor. This cage was free of all furnishings. In comparison with groups 1 and 2, these rats had minimum opportunity for proprioceptive and visual experience.

Each cage had very good illumination provided by standard fluorescent lamps located above each cage. An extra lamp with a 100-w. daylight bulb was placed over cage 3 to compensate for the lower reflecting surface of that cage. From this description it can be seen that differences in illumination per se among the three cages were almost certainly negligible. Although other experiential differences, such as cutaneous experiences, probably existed, our main concern was to vary visual-proprioceptive experience with inanimate stimuli, while controlling other factors that might influence the animals' behavior on our tests.

The three groups were treated alike in all other respects. The lights were turned off at night. Food and water were located in the center of each cage. All rats were handled twice a month when their cages were cleaned.

During periodic day and night observations striking differences in behavior were noticed among the three groups. Group 1 animals were most active and would often run to more secluded areas, such as under a tunnel, when *E* approached the cage. Group 2 animals were less active. However, they frequently attempted, in vain, to scale the glass walls which separated them from the white objects. Group 3 animals, the least active of all, would usually hug the sides of the cage. The distribution of feces in the different pans verified these observations.

After they had lived in these different environments for 60 days, all the rats were transferred to smaller laboratory cages 18 in. long, 12 in. wide, and 10 in. high. Since two rats had died in each group, we were left with 12 animals per group. Six animals were placed in each of six laboratory cages.

The next day, when the rats were approximately 85 days old, a 23½-hr. food-deprivation schedule, which lasted 7 days, was begun. The rats were fed wet Purina mash for 30 min. daily. During this week they were also handled extensively. At the conclusion of this deprivation schedule, three series of experiments were performed. All daily tests were run after a 23½-hr. food-deprivation period.

EXPERIMENT I

Procedure

The apparatus, an elevated maze, is shown in Figure 1. The stem was 18 in. long, and the four arms were 16 in. long and 4 in. wide. The maze was made of unpainted pine wood. The rat could enter any of the four goal boxes by easily pushing open a vertically suspended black door. There was wet Purina mash in each of the four goal boxes.

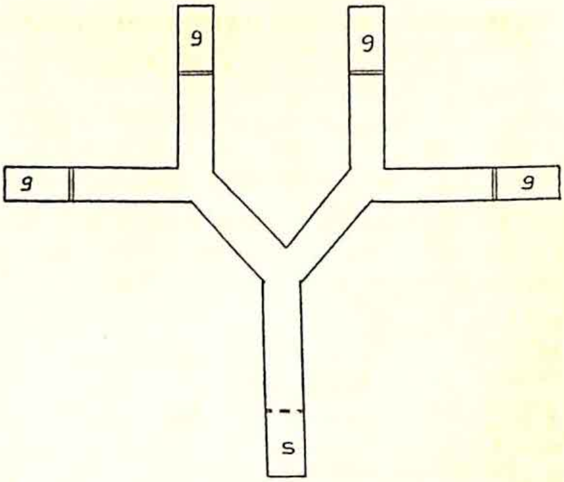

FIG. 1. Floor plan of maze used in Experiment I. *S*—starting box; *g*—goal boxes; = = =—sliding door; = —swinging doors. (For further explanations see text.)

During the first day of this experiment, the rat was placed in the starting box and permitted to explore the maze for 7 min. If *S* entered a goal box, it was permitted to nibble at the food for 15 sec. and was then returned to the starting box. This sequence was repeated until the 7 min. had elapsed.

Three sets of scores were recorded: (*a*) the *latency* of the first response, i.e., the time that elapsed before the rat left the starting box; (*b*) an *activity* score, i.e., the number of 16-in. units traversed during this 7-min. period, and (*c*) an *emotionality* score, i.e., the number of defecations during the same period.

On the second day a test of *variability* of behavior was begun. In this test, the rat was given 20 trials—2 on the first day, 3 on the second day, and 5 on the third, fourth, and fifth days. Food was available in each of the four goal boxes. The path chosen on each trial was recorded. The criterion of variability was the number of times the animal chose a different path on successive trials. Since there were 20 trials, the maximum variability score was 19.

Results

The results of Experiment I are presented in Table 1. After the analysis of variance was performed for each subtest, we utilized Tukey's technique (10) to determine whether the differences between pairs of means were significant. It is quite clear, from a comparison of the values in the last row of Table 1 and the respective mean differences, that there were no significant differences, at the .01 level, between the complex visual-proprioceptive group (group 1) and the complex visual but minimum proprioceptive group (group 2) on these tests. These two groups could therefore be considered as coming from the same population. The

TABLE 1

Analyses of Variance between the Means Obtained for the Three Groups on the Latency, Activity, Emotionality, and Variability Tests

GROUP	*N*	LATENCY*		ACTIVITY		EMOTIONALITY		VARIABILITY	
		Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
1	12	0.89	0.44	26.08	12.22	1.04	1.24	15.67	2.84
2	12	1.06	0.28	25.25	9.67	1.08	1.28	15.08	3.05
3	12	1.91	0.41	8.17	10.94	2.83	0.99	9.33	5.10
F		25.74		10.14		9.08		13.77	
p		<0.001		<0.001		<0.001		<0.001	
Required diff. between pairs of means		0.245		7.5		0.79		2.47	

* Transferred to logarithmic units.

TABLE 2

Analysis of Variance of the Distribution of Errors Obtained from the Form-Discrimination Test

STATISTIC	GROUP 1	GROUP 2	GROUP 3
Mean	35.00	25.08	92.50
SD	3.54	5.30	6.64
F		562.99	

TABLE 3

Comparison of the Error Scores Obtained from the Form-Generalization Test

STATISTIC	GROUP 1	GROUP 2	GROUP 3
N	12	12	12
Mean	0.83	0.75	10.17
SD	0.85	0.87	1.12

combined group (1 and 2) was clearly superior to the minimum visual-proprioceptive group (group 3).

EXPERIMENT II

Before these series of tests were begun, the animals were permitted three days without tests, during which time food was always available in their cages. On the fourth day a series of visual form-discrimination tests was started.

Procedure

We used an elevated visual discrimination apparatus, resembling the one described by Brown and Ghiselli (1), with the exception that we used four units and eliminated the shock. The entire apparatus was 92 in. long and the width of the runway was 4 in. The rat was placed in the starting box and ran to the bifurcation from which it was to make its choice. If *S* chose the "correct" form, it could push through the one-way door very easily. The incorrect choice led to a door which was held closed by a latch. The discrimination cards were fitted directly on the door. There were four possible errors in any one trial. The correction method was used and back-tracing was not scored an error. After the fourth correct choice on each trial the rat was permitted to nibble Purina mash in the goal box for 15 sec. This apparatus was designed to foster rapid form discrimination and generalization. This was done by using four units, fitting the cards on the door through which the rat entered the next unit, and keeping the size of the forms within the rat's visual angle from the bifurcation point (cf. 8). That our anticipation was realized is shown by the fact that we obtained immediate generalization to forms rotated 90°, especially in the case of groups 1 and 2 (see Tables 3 and 4), although Fields (2) could only achieve the same result with great difficulty.

The following three tests were performed using this discrimination apparatus:

Form discrimination. The animals were given four trials per day. All forms were white on a black background. For half the animals in each group a triangle with apex upright was the positive form; for the other half a U was the positive form. A circle was the negative form for all animals. The forms were equated as nearly as possible for size. The criterion of learning was 9/10 errorless trials.

Form generalization. After the animals had successfully learned to make the discrimination, the forms were rotated clockwise through 90°. The number of errors the rat made in 20 trials was recorded.

Form generalization with a new negative form. Since the results of the second test might merely have indicated that the animal was avoiding the negative figure, the forms were rotated clockwise through 90°, using a new negative form. The new negative form was a U for the animals for which the triangle was positive, and a triangle for the remaining animals. Again, the number of errors in 20 trials was recorded. One rat in group 2 died before this test was completed.

Results

The results of the form-discrimination test are presented in Table 2. Group 2 was superior to group 1, which, in turn, was superior to group 3. These differences are significant at the .01 level ($p < .001$; required difference between pair of means for significance at the .01 level, based on Tukey's analysis, 3.51).

The results of the form-generalization test are shown in Table 3. Since Bartlett's analysis indicated that the variances of the three groups were not homogeneous, we could not perform an analysis of variance. The t ratio obtained from a comparison of the means of groups 1 and 2 was not significant ($p > .1$), allowing us to combine groups 1 and 2, which combination was clearly superior to group 3 ($p < .001$).

TABLE 4

Comparison of the Errors Made in Form Generalization with the New Negative Form

STATISTIC	GROUP 1	GROUP 2	GROUP 3
N	12	11	12
Mean	7.08	4	20.83
SD	4.88	4.62	4.59

Although the mean errors per group were larger for the form-generalization test with a new negative form, the trend was similar to that of the previous test, as can be seen from an inspection of Table 4. Again, there was no significant difference between the means of groups 1 and 2 ($p > .1$). Groups 1 and 2 combined were superior to group 3 ($p < .001$).

EXPERIMENT III

Before this experiment was begun the animals were permitted to rest for seven days without tests.

Procedure

A technique similar to the one Maier (9) used in his reasoning tests was employed for this test of spatial problem-solving ability. The apparatus consisted of a number of open elevated platforms 4 in. wide.

The rat was first placed at a point where it could see the food through a glass barrier. This was position *S*. The animal was then permitted to go to position *B* by running away from the glass and making three left turns, traversing 95 in. in all. This constituted experience 1. The animal was removed from the maze and replaced at position *B* 30 sec. later, and allowed to go to the goal box by running straight forward and then making a left turn, covering a total distance of 39 in. This was experience 2.

The third and critical trial was given to determine whether the animal "grasped" the spatial relationships which would enable it to select a much shorter path to the goal by taking a diagonal route from the second turning point, or whether it would merely combine experience 1 and 2 and take the long path to the goal. The distance to the goal via the short path was 66 in., whereas it was 134 in. via the long path. The number of animals in each group which took the short path on the critical trial was recorded.

Results

Ten of the 12 animals in group 1, 9 of the 11 animals in group 2, and 2 of the 12 animals in group 3 chose the short path on the critical trial.

A chi-square test comparing groups 1 and 2 was not significant, but the chi-square value comparing the frequencies of combined groups 1 and 2 and group 3 was significant ($p < .001$). It was concluded that the animals that had the complex visual environment were clearly superior, in spatial problem solving, to the animals that had a simple visual environment.

At the conclusion of the research, the rats were approximately 131 days old. The weight records showed that the average losses and gains were similar for all three groups. Throughout the course of the experiment the rats' diet was supplemented by lettuce and vitamins and they appeared healthy throughout the experiment.

DISCUSSION

The following conclusions may be drawn from the results:

1. The four tests of Experiment I did not detect any differences between groups 1 and 2. The combined group (groups 1 and 2) was clearly superior, by these criteria, to group 3; i.e., they responded earlier, were more active, defecated less frequently, and displayed greater variability of behavior when placed in a novel situation (an elevated maze). It is supposed that the performance on these tests was largely affected by the degree of insecurity generated in an unfamiliar environment. It is reasonable to infer that a rich visual experience during infancy is a positive factor in developing adaptive behavior since the greatest common factor in the early environments of groups 1 and 2 was, presumably, the complex visual field.

2. Group 2 learned to discriminate the visual forms faster than group 1, which, in turn, had a faster learning rate than group 3. There were also no differences between groups 1 and 2 on the form-generalization test. Once again combined groups 1 and 2 were superior to group 3.

3. The combined visual group (groups 1 and 2) was superior to the impoverished visual group (group 3) on the spatial problem-solving test. Once again, no difference was detected between the animals which presumably had had much opportunity for proprioceptive experience (group 1) and those which had had relatively less opportunity for proprioceptive experience (group 2).

We will confine our discussion to an interpretation of the two most important findings. The first finding is that the animals of groups 1 and 2, which were reared under similar conditions (especially with respect to visual experience), behave in similar ways. The animals of group 3, reared under dissimilar conditions of breadth of visual experience, were "inferior" to groups 1 and 2 on emotionality, discrimination, and problem-solving tests. From these findings we may draw two reasonable interpretations. First, the differences in experience apparently produced differences in the emotionality of the two groups (1 plus 2 vs. 3). It would seem that the restricted visual experience of group 3 was at least partly responsible for the "insecurity" of these animals when they were placed in our open-test conditions. Their emotional behavior probably also influenced their performance on the other tests. The difference in visual experience, presumably, produced differences in discrimination and problem-solving behavior also. This difference is readily attributable to differences in perceptual learning during their development. This is in keeping with previous findings and interpretations (3, 4, 6).

The second fact which must be discussed is the reported difference between groups 1 and 2 in the *rate* of learning to discriminate visual forms. The author feels that this is an important finding, especially since there was very little overlap in the error scores; i.e., most of the animals in group 2 made fewer errors to reach the criterion than the animals in group 1.

In his early work Krechevsky (7) claimed that an animal exhibits specific "hypotheses" during the presolution period of a problem situation. In a subsequent paper Witkin (11) criticized Krechevsky, pointing out that it is only in "insoluble" problems that these "hypotheses" are exhibited. Witkin does, however, state that animals do adopt systematic responses in problem-solving behavior, especially when the situation is well differentiated. "The systematic responses by each animal seem to represent rather stable preferences of that animal. Apparently each rat demonstrates a number of such preferences or '*reaction sets*' " (11, p. 336, italics mine). It is precisely this notion of "reaction set" which we wish to develop here. The form-discrimination test consisted of an open-field situation. There were many possible ways of attempting to solve the problem; i.e., many different stimuli were impinging upon the organism, many of them irrelevant to the problem. We knew further that form discrimination is very difficult and artificial for the rat. We would thus argue that, since group 2 animals were physically, but not visually, restricted during their development, there was a greater tendency that visual stimuli would be perceptually *prominent* (cf. 11, p. 335) for them. Since group 1 animals had a much freer exploratory experience during development, it seems very reasonable to expect that other stimuli (e.g., kinesthetic) were also perceptually prominent for them. It is the time it took to eliminate these incorrect perceptual responses which would account for the longer time it took group 1 animals in the form-discrimination test. We wish to stress that it was not that one group was inferior to the other in visual discrimination ability but that more stimuli were perceptually prominent for group 1.

SUMMARY

This paper was concerned with determining whether various infant experiences of rats produce differences in behavior at maturity.

Three groups of male hooded rats were reared under three different conditions. Group 1 had a complex visual-proprioceptive environment. The environment of group 2 offered much opportunity for visual experience but little opportunity for proprioceptive experience. Group 3 had a relatively homogeneous visual-proprioceptive environment. At maturity, the groups were given three series of tests.

From our results we concluded that early experience and learning is an important determinant of the emotionality and cognitive ability of adult rats. The differences were illustrated by the rats' performance in tests of emotion, form discrimination and generalization, and spatial problem solving. It is further suggested that the quality of the animals' infant experience will determine the kinds and number of "hypotheses" they can test when solving a problem at adulthood.

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Received November 13, 1953.

SITUATIONAL DETERMINANTS OF THE RELATIVE DIFFICULTY OF SIMULTANEOUS AND SUCCESSIVE DISCRIMINATION

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In an attempt to reconcile conflicting evidence on the relative difficulty of simultaneous and successive problems in two-choice discriminative situations, Bitterman and Wodinsky (3) proposed the following principle: any condition which favors the functional isolation of the two members of each pair of stimuli (component organization) will facilitate the simultaneous solution and retard the successive solution, while any condition which favors the perception of each pair as a whole (configurational organization) will retard the simultaneous solution and facilitate the successive solution. The present experiment provides a systematic test of the validity of this principle. Simultaneous and successive problems were presented in a four-window jumping apparatus in such a way as to foster either component or configurational organization. To promote component organization, the two members of each pair of stimuli were separated in space, and the animal was required to make a direct approach to one member of each pair. To promote configurational organization, the two members of each pair of stimuli were spatially contiguous, and the animal was required to jump away from (to the right or left of) each pair. In all, four groups of animals were trained, one on each of the two types of problem (simultaneous and successive) under each of the two perceptual conditions. Another important feature of the design should be noted: each group learned, not one, but two consecutive problems of the same type in counterbalanced order, a procedure which provided data on shifts in relative difficulty from the initial problem to the second. A study by Bitterman and McConnell (2) suggested that it may be possible in this way to distinguish between intrinsic differences in difficulty and transient differences due to the readiness with which particular sets can be adopted under the various experimental conditions.

METHOD

Subjects

The *S*s of the experiment were 48 experimentally naive, albino rats bred in the laboratory. The animals were between three and four months old at the beginning of the work.

Apparatus

A four-window jumping apparatus was employed in the experiment. The windows, 5.5 in. square, were cut into the panels of a hemioctagonal surround, and a circular jumping platform was so situated that its perimeter was equidistant from the four windows. As in the conventional jumping apparatus, behind the windows there was a feeding platform and below them was a net into which the animal fell after an incorrect response. The entire apparatus was painted flat black. The experimental design called for five different kinds of stimulus cards: (*a*) homogeneous mid-gray; (*b*) black-and-white vertical stripes (the width of each stripe being 0.5 in.); (*c*) black-and-white horizontal stripes (the width of each stripe being 0.5 in.); (*d*) small black circle (1 in. in diameter) centered on a white ground; and (*e*) large black circle (4 in. in diameter) centered on a white ground.

Preliminary Training

At the start of the experiment the animals were placed on a 24-hr. feeding schedule. After adjustment to handling, they were fed on the feeding platform and taught to jump gradually increasing distances from the jumping platform to the open windows at the extreme left and right only, manual guidance being employed to provide equal experience with both. The two center windows were open but unused—the animals were not trained to jump to them, nor were they selected spontaneously. At the conclusion of the preliminary training the animals were divided into four groups of 12 animals each, matched for sex, weight, and adjustment to the apparatus.

Discriminative Training

One group of animals, which will be designated the *simultaneous-component* group, learned two consecutive simultaneous discriminations (between horizontal and vertical stripes and between large and small circles) under conditions designed to promote component organization. The two cards to be discriminated in each problem were placed in the extreme left and right windows, with the animal being required to jump directly at one of the two cards on each trial. Thus, the two card arrangements of the horizontal-vertical problem were (reading from the extreme left to the extreme right window) *HGGV* and *VGGH*, where *H* stands for a horizontally striped card, *G* for a gray card, and *V* for a vertically striped card. Similarly, the two card arrangements for the circle discrimination were *LGGS* and *SGGL*, where *L* stands for large circle and *S* for small. Six of the animals in this group learned the horizontal-vertical discrimination before the circle discrimination, while the remaining animals learned the two problems in reverse order. Of the 12 animals, 3 (selected at random) were rewarded for jumping to horizontal stripes and large circle (i.e., for jumping right to *VGGH* or *SGGL* and left to *HGGV* or *LGGS*), 3 were reinforced for jumping to vertical stripes and large circle, 3 to horizontal stripes and small circle, and 3 to vertical stripes and small circle. Ten trials per day were given by the correction method. Each trial consisted of a series of one or more jumps to a given set of cards, the trial being terminated by a correct response. A maximum of three free jumps was permitted on each trial, and after three consecutive errors the animal was manually guided in the correct direction. The criterion of learning on each problem was one errorless day, and on the day after an animal reached criterion on its first problem, training on the second was begun.

A second group (*successive-component*) learned two consecutive successive discriminations under conditions designed to promote component organization. Again, the cards to be discriminated were placed in the extreme right and left windows and directly approached by the animals. The two card arrangements of the stripe problem were *HGGH* and *VGGV*, while those of the circle problem were *LGGL* and *SGGS*. In all other respects the training of this group was analogous to that of the simultaneous-component group. Half the animals learned the circle discrimination before the stripe discrimination, and half learned the two problems in the reverse order. Three of the animals were reinforced for jumping right to *HGGH* or *SGGS* and left to *VGGV* or *LGGL*, three for jumping right to *VGGV* or *SGGS* and left to *HGGH* or *LGGL*, three for jumping right to *HGGH* or *LGGL* and left to *VGGV* or *SGGS*, and three for jumping right to *VGGV* or *LGGL* and left to *HGGH* or *SGGS*.

A third group of animals (*simultaneous-configurational*) learned two consecutive simultaneous problems under conditions designed to promote configurational organization. The cards to be discriminated were placed in the two center windows, and the animal was required on each trial to approach one of the two gray cards which were situated in the extreme right and left windows. Thus, the two card arrangements of the stripe problem were *GHVG* and *GVHG*, and those of the circle problem were *GLSG* and *GSLG*. In general, the training of this group was directly analogous to that of the simultaneous-component group except that, instead of being reinforced for jumping to one of the discriminanda (e.g., *H*) in one of the end windows with gray cards in the center windows, the animals were reinforced for jumping to a gray card in the end window adjacent to that one of the two center windows which contained *H*.[1]

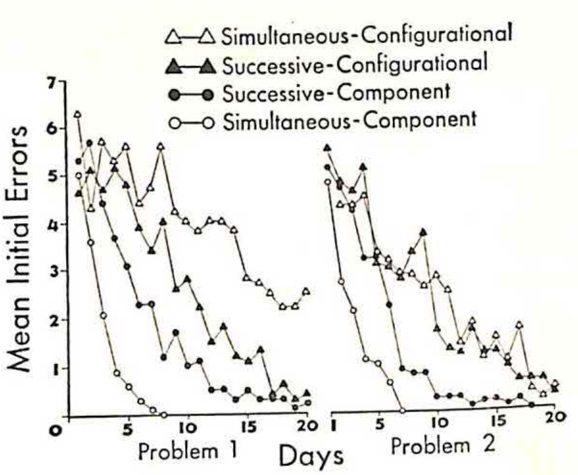

FIG. 1. The course of learning in the four groups during the first 20 days on each problem. To conserve space the tails of the curves are omitted. It is to be noted that the curves are based on the whole group at each point. The assumption was made that once an animal reached the criterion, its performance thereafter would have been errorless had it been tested, and so it remained in the denominator for the computation of means.

A fourth group (*successive-configurational*) learned two consecutive successive problems under conditions designed to promote configurational organization. The cards to be discriminated were placed in the two center windows, and the animals were required to approach one of the two gray cards situated in the extreme right and left windows. The two card arrangements of the stripe problem were *GHHG* and *GVVG*, and those of the circle problems were *GLLG* and *GSSG*. The training of this group was analogous to that of the successive-component group except that, instead of being reinforced for jumping directly to one of the discriminanda in one of the end windows, the animals jumped to one of the gray cards in the end windows, depending upon which pair of discriminanda appeared in the center windows.

RESULTS

The course of learning in each of the four groups is shown in Figure 1, and in Tables 1 and 2 the performance of each group on each of the two problems is summarized in terms of mean initial errors and mean total (initial plus repetitive) errors. The dependence of the relative difficulty of the simultaneous and successive problems on situational variables can be seen clearly in the data. Under component conditions the initial simultaneous problem is significantly easier than the initial successive, while under configurational condi-

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[1] While in all the other groups six animals learned the discriminations in the order stripes-circles, and six in the order circles-stripes, seven animals of the present group began with stripes and only five with circles.

TABLE 1

Mean Initial Errors Made by Each of the Four Groups in Each of Two Consecutive Problems

GROUP	PROBLEM 1	DIFF.	p*	PROBLEM 2	DIFF.	p*	PROBLEM 2 — 1	p**
Simultaneous-component	12.58			12.17			0.41	
		22.09	.01		14.91	.01		
Successive-component	34.67			27.08			7.59	
		21.16	.05		20.09	.01		
Successive-configurational	55.83			47.17			8.66	
		51.58	.01		3.58			
Simultaneous-configurational	107.41			50.75			56.66	.05

* Significance estimated by Wilcoxon's nonparametric test for unpaired replicates (4).

** Significance estimated by Wilcoxon's nonparametric test for paired replicates (4).

TABLE 2

Mean Total Errors Made by Each of the Four Groups in Each of Two Consecutive Problems

GROUP	PROBLEM 1	DIFF.	p*	PROBLEM 2	DIFF.	p*	PROBLEM 1 — 2	p**
Simultaneous-component	20.25			18.00			2.25	
		32.67	.01		16.42	.01		
Successive-component	52.92			34.42			18.50	.01
		36.58	.01		25.75	.01		
Successive-configurational	89.50			60.17			29.33	
		66.66	.02		8.33			
Simultaneous-configurational	156.16			68.50			87.66	.02

* Significance estimated by Wilcoxon's nonparametric test for unpaired replicates (4).

** Significance estimated by Wilcoxon's nonparametric test for paired replicates (4).

tions the reverse relation obtains between the two types of problem. In both conditions, however, the difference between the more difficult problem and the less difficult problem tends to decrease with practice. This change in relative difficulty is most marked under configurational conditions, with the difference between simultaneous and successive presentations disappearing entirely in the second of the two consecutive problems. Under component conditions the performance of the simultaneous group continues to be superior in the second problem, but the significant decline in total errors shown by the successive group indicates a trend toward decreased relative difficulty. Under component conditions in the two-window jumping apparatus (1, 2) the difference in difficulty between simultaneous and successive presentations disappears in the second of two successive problems (involving the same discriminanda as here employed), which suggests that increased separation of the stimuli presented in the end windows of the four-window apparatus makes a stable configurational set more difficult to achieve. It seems likely, however, that even in the four-window apparatus the simultaneous vs. successive difference should eventually disappear in the course of a longer series of problems.

From the point of view which led to the design of the present experiment, the only really surprising result is the significant and consistent superiority of the successive-component group as compared with the successive-configurational group. On the assumption that both successive problems would be mastered in terms of the difference between configurations, the opposite outcome was anticipated. It is conceivable that the relevance of the discriminanda is more readily apparent under conditions of direct approach, and that this difference more than compensates for the difference in the readiness with which a configurational organization may be achieved. It is conceivable also that the processes underlying solution of the two successive problems are quite distinct. In any event, the reason for the persistent difficulty of the successive-configurational problem is not yet clear.

SUMMARY

Each of four groups of rats learned two consecutive problems in a two-choice discriminative situation. Two groups were trained under conditions designed to facilitate the perceptual analysis of each pair of stimuli into *components*—the two members of each pair were separated in space, and the animal was required to jump directly to one member of the pair on each trial. The remaining two groups were trained under conditions designed to promote perception of each pair of stimuli as a whole (*configuration*)—the two members of each pair were spatially contiguous and the animal was required to jump to a window at the right or left of the pair. Under component conditions successive discrimination was more difficult than simultaneous both in the first and in the second of the two consecutive problems, although there was some tendency for the difference in difficulty to decline from the first problem to the second. Under configurational conditions the simultaneous discrimination was more difficult in the first of the two problems, but the difference disappeared in the second (due principally to the marked improvement in the performance of the simultaneous group). In both problems the successive discrimination was more difficult under configurational as compared with component conditions.

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Received November 2, 1953.

CHANGE IN STIMULUS CONDITIONS AS A DETERMINER OF "REGRESSION" IN THE RAT[1]

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Experimental investigations of "regression" in the rat ordinarily involve establishment of one response (e.g., a right turn in a T maze) and reversal training in which Response I is replaced by an incompatible response (II) (e.g., a left turn). A noxious stimulus (usually electric shock) is then introduced, and if Response I occurs, *S* is said to have regressed.

The studies may be classified either as Type P experiments, in which the noxious stimulus introduced on test trials precedes the choice response (e.g., 1, 3, 7), or as Type F experiments, in which the noxious stimulus follows the choice (4, 8). Since the experiment reported below deals with the effects of a change in stimuli presented before the choice response, it is most relevant to Type P studies.

No Type P study of which we are aware provides evidence of regression significantly above chance. Little importance should be attributed to regression of less than half the *S*s (in a two-choice situation) because such results could be attributed entirely to the absence of transfer from training to test (shock) trials. If the response to which *S* regresses was an original preference, as in Aebli's study (1), absence of transfer could explain regression in more than half the *S*s on the further assumption that the same preference would have been exhibited to the test stimulus had it been presented before training. Even though there is no clear evidence of regression in more than 50 per cent of the *S*s in a Type P experiment, it seems probable (especially in view of the results to be reported below) that such data could be obtained under appropriate conditions even if regression were not to an original preference.

The present experiment was designed as a control to determine if regression might result from a *change* in stimulating conditions at the choice point rather than the introduction of a *noxious* stimulus.

METHOD

Subjects

The *S*s were 49 male albino rats from the Kent State University colony. All *S*s were between five and eight months old at the beginning of the experiment.

Apparatus

The apparatus was a single-choice-point alley T maze with interchangeable parts. The distance from starting box to choice point was 24 in.; from choice point to either end box was 25 in. Guillotine doors controlled by *E* were placed at the exit from the starting box, at the choice point, in each arm 9 in. from the choice point, and at the entrance to the end boxes. Black cloth curtains were placed in each arm 5 in. from the end boxes.

Two stem sections were used. One was unpainted pine and contained a hardware cloth hurdle 6 in. long and 2 in. high which was placed next to the choice point. The other stem section was painted black and contained no hurdle. There were two sets of maze arms which differed only in that one was painted black while the other was unpainted.

Procedure

Training was initiated three or more days after the animals had been on a schedule of a 1-hr. feeding period (unlimited food) every 24 hr. Throughout the experiment all *S*s were run immediately before their daily feeding.

For the two experimental groups, training on Response I consisted of 10 trials a day for 10 days, a total of 100 trials. On each trial one of the unpainted goal boxes containing a .3-gm. pellet of Purina Fox Chow (*S*'s regular diet) was placed at the end of the arm which had been arbitrarily designated as correct. The black box without reward was at the end of the other arm. The unpainted alley sections were used throughout training. During this portion of training the intertrial interval was approximately 10 min. Throughout the experiment, the noncorrection technique was used. Doors were closed behind *S* as soon as it touched the curtain on both "correct" and "incorrect" choices. On nonrewarded runs, the animal was left in the black end box 60 sec. before being removed. Half the *S*s were trained to the right and half to the left. No errors occurred on the last few days of Response I training.

Twenty-three hours after training on Response I was completed, the animals were trained in the opposite direction (Response II). For this training, the end boxes were interchanged so that the unpainted box contained the reward on all trials. During the acquisition of Response II, the intertrial interval was the time required to return the animal to the starting box. The short

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[1] This study was reported at the 1950 meeting of the Midwestern Psychological Association in Detroit. Groups E-1 and C were run as a part of a master's thesis study by J. R. T. The authors would like to express their thanks to Anthony J. Cacioppo for running the *S*s in group E-2.

[2] Now at Michigan State College.

TABLE 1

Summary of Results Indicating the Total Number of *S*s, the Number of *S*s Making Response I, the Number Making Response II, and the Percentage Making Response I for Each Group and for the Two Experimental Groups Combined

GROUP	*N*	RESPONSE I	RESPONSE II	PERCENTAGE RESPONSE I
E-1	26	16	10	62
E-2	10	8	2	80
Exper. total	36	24	12	67
Control	13	1	12	8

intertrial interval was used on the assumption that it would facilitate a rapid shift to Response II. This training was continued until a criterion of five successive correct responses was reached.

The test run followed immediately after the second response had been learned to the criterion. For group E-1 the conditions were changed by replacing the unpainted stem of the maze by the black stem without the hurdle. Also, the black end box was replaced by a second unpainted end box, and food was placed in both end boxes. The test trial always followed the last training trial within 90 sec. The test runs for group E-2 were the same as for group E-1 except that instead of a change in the stem section, the black arms were substituted for the unpainted ones.[3]

In the control group, 15 reinforced trials in a straight runway were substituted for the Response I training of group E-1. Starting with Response II training the procedure for these *S*s was identical to that used with group E-1. All three groups required approximately the same mean number of trials to reach the criterion of 5 successive correct trials on Response II. The number of runs required to meet this criterion ranged from 7 to 15, excluding criterion trials.

The groups were not run simultaneously so that minor differences in handling, room temperature, etc. probably were involved.

RESULTS

The results are summarized in Table 1. As shown there, 16 (62 per cent) of the 26 *S*s in group E-1 regressed as did eight of the 10 *S*s in group E-2. The results from group E-1 do not differ significantly from chance (50 per cent); those for group E-2 fall just short of differing significantly from chance at the 5 per cent level of confidence (single-wing hypothesis for expansion of the binomial). Combining the results of the two experimental groups indicates a preference for Response I, which differs from chance at the 4 per cent level of confidence as determined from the standard error of a proportion with the correction for continuity (2, p. 58).

The perseveration in Response II of 12 of the 13 control *S*s indicates that there was transfer from training to test situation. Thus, if no regression occurred, more than 50 per cent of the *S*s would have made Response II. Therefore, it seems safe to conclude that there is a reliable tendency for rats to revert to Response I under the particular conditions of this experiment.

DISCUSSION

The results of the present study offer rather clear evidence of regression in the rat in a Type P experiment. Since the factors operating in this study may well have been operating in other Type P studies, it appears that the introduction of a change in stimulus condition (qua change) may have been entirely responsible for the regression obtained in other Type P studies.

It could be argued that the black alleys introduced on the test trial were noxious because they were the same color as the negative box. However, the black end box would have slight noxious properties compared with an electric shock, and there would be incomplete and probably only slight generalization of these properties from the end box to the alleys. Since shock produced more regression than a buzzer in Sanders' study, it would appear that *if* the noxiousness of the stimulus causes regression, there is a positive relationship between degrees of noxiousness and the percentage of regressive responses. However, in the present study, we obtained an unusually high percentage of regressive responses with the introduction of a stimulus which, if noxious, is only slightly so compared with an electric shock. Thus, while it is unfortunate that the stimulus complex introduced on our test trial might have had slight noxious properties, this does not seriously weaken our interpretation that the change in stimulation was responsible for regression.

As pointed out by Saltz (6), O'Kelly's finding (5) that six of seven rats regressed when they were shifted from a thirst drive to

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[3] We added group E-2 rather than running more *S*s in group E-1 in hopes that this change would produce a greater percentage of "regressive" responses. Although our assumptions that a change in the arms was more distinctive than a change in the stem section, and that a greater change in stimulus conditions would lead to more regression, are tenuous, they tend to be supported by our findings.

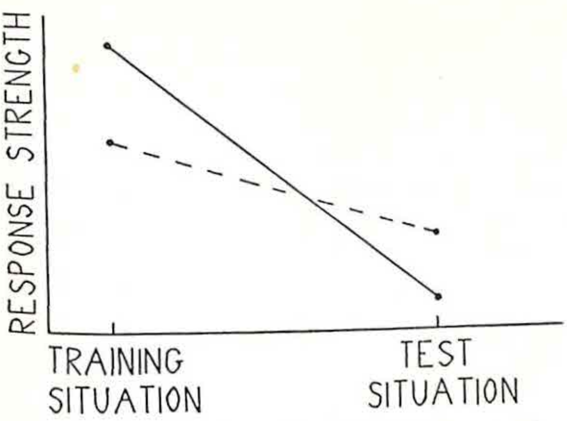

FIG. 1. Representation of the differential generalization explanation of the results. Stimulus generalization of Response II is represented by the solid gradient. The dashed line is the generalization gradient for Response I. In the training situation Response II is dominant (solid gradient is higher); under test conditions Response I is dominant.

satiation also supports the interpretation that a change in stimulating conditions may lead to regression even if the change is not noxious.

The reversion to Response I in the present study may be explained in at least two ways. It may be attributed to disinhibition of the effects of extinction of Response I during the reversal training, or it may be derived from the assumption that stimulus generalization resulting from training of Response I is broader than generalization of the reversal (Response II) training. This differential generalization explanation is represented in Figure 1.

It should be noted that this explanation differs from the simple assumption that there is inadequate transfer from training to test situation. The differential generalization interpretation can explain regression significantly above chance (50 per cent), while the lack-of-transfer interpretation can only explain regression to chance performance (when there is no original preference).

The differential generalization explanation, which seems more satisfactory as it can also be used to derive disinhibition, may be made more specific by any one of several different assumptions, namely: (*a*) broader generalization of older habits than of newer habits, (*b*) broader generalization of effects of reinforced trials than of extinction effects (Response I is extinguished during reversal training), or (*c*) the effects of some other variable on the slope of the generalization gradient. Saltz (6) has presented a theory to explain regression and several other phenomena in terms of the second type of generalization theory. Our findings can be predicted from his theory but do not serve as a test between his and other types of generalization explanations.

Sanders' experiments (7) may be interpreted as supporting the differential generalization explanation. She obtained the highest percentage of regression with a shock within the maze, the next highest percentage of regression with a loud sound, and little or no regression with shock outside the maze, injection of caffeine, or injection of adrenalin. It would appear that within the limits observed there is a positive relationship between the distinctiveness of the novel stimulus at the time of the choice and percentage of regression.

SUMMARY

An experiment was conducted to determine if a nonnoxious change in stimuli at the choice point might lead rats to shift from a recently acquired response (e.g., right turn) to an older response (left turn). Two-thirds of the *S*s reverted to the older response. The results suggest that regression resulting from an electric shock at the choice point, which other *E*s have reported, is not dependent upon the noxious nature of the change in the stimulus complex which is introduced.

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Received October 10, 1953.

A COMPARISON OF CHEMICAL AND MECHANICAL ALTERATIONS OF SEIZURE PATTERNS IN MICE[1]

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During the past several years, one of us has been primarily concerned with the effects of changes in the stimulus pattern as related to seizure incidence and latency in genetically susceptible mice that characteristically react to a white noise above 86 db by exhibiting clonic-tonic convulsions which, in the majority of cases, prove fatal (3, 4). The other has studied the effects of metabolically active substrates and enzyme inhibitors on the same behavior reaction (6, 7, 8). In the present paper one particular stimulus pattern is compared with a substrate producing some similar effects, and the two are used in combination in an attempt to elucidate the mechanism of action of each.

It has been shown that after a 20-sec. priming stimulus and 10-sec. interruption followed by 90 sec. of sound stimulation, there is a decrease in susceptibility to convulsions as compared with continuous stimulation (3). It has also been demonstrated that glutamic acid reduces the convulsive risk and increases survival in several susceptible strains, that this effect can be counteracted by structural analogues of glutamic acid, that adaptation to glutamic acid occurs upon repeated administration, and that the response of the two sexes to this substrate differs in the DBA/1 strain (6, 8). There are two major points of similarity resulting from the two procedures: (*a*) a reduced seizure incidence, and (*b*) a reduced incidence of fatalities among animals that convulse. The differential response of the two sexes obtained with glutamic acid is, on the other hand, not a sequel to interrupted stimulation.

It should be pointed out that the experiments with glutamic acid reported in this paper were carried out by Fuller and Craig, and represent an independent corroboration of results reported by Ginsburg *et al.* (6, 7, 8).

METHOD

Subjects

Genetically homogeneous mice of the DBA/1 strain, raised by the supply department of the R. B. Jackson Laboratory, were used as test animals. These have been produced by over 100 generations of brother × sister matings and are known to be approximately 60 per cent susceptible to seizures during the period from 30 to 45 days of age, when subjected for 1½ min. to a white noise at intensities of 86 to 104 db. The animals were fed a diet of Purina Laboratory Chow and had access to food and water at all times. Animals conspicuously above or below average body size were discarded and not tested.

Apparatus and Procedure

Only first trials are reported in this paper. Mice were tested between the ages of 30 and 35 days, using the method described by Fuller (4), as modified from Hall (9). A standard doorbell is suspended by rubber bands above a galvanized iron washtub, 60 in. in circumference at the bottom. The tub is enclosed in a box packed with shavings, and a hinged frame with double-thickness Lucite windows covers the apparatus. Tests with a sound meter showed an average sound pressure of 95 db during these experiments, with variations in intensity of about 1 db between different parts of the enclosure. Illumination is provided by a 75-w. bulb suspended about 3 ft. above the hinged cover. A complete record of behavior was made during each test. The times of onset of wild running, convulsion, and death or recovery were recorded, using a stop watch. Convulsions which occurred were classified in order of severity as clonic-tonic, clonic, and convulsive spasms (2).

For the glutamic acid test a neutral solution of 1(+) glutamic acid (pH 7.4) was prepared in the manner described by Marx (10) at a concentration of 200 mg. per cubic centimeter; it was administered by subcutaneous injection at a volume of 0.1 cc. per 10 gm. of body weight 30 to 45 min. before testing. Control animals were handled in exactly the same way but received an equal volume of 0.9 per cent sodium chloride. The interrupted stimulus followed the schedule of 20 sec. of bell ringing, 10 sec. of silence, and 90 sec. of bell ringing. It

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[1] These studies were aided by contracts between the Office of Naval Research, Department of the Navy, the University of Chicago (NR 110–500) and the Roscoe B. Jackson Memorial Laboratory (ONR 1001 [01]).

[2] The authors gratefully acknowledge the technical assistance of Mr. John Craig.

TABLE 1

Convulsion Data for the Eight Groups of Mice

GROUP	SEX	N	CONVULSION TYPE			TOTAL	DIED	DEATH/ CONVULSIONS	MEAN LATENCY (SEC.)	*SD* OF LATENCY
			CT	C	CS					
CS-S	♂	50	43	2	2	47	43	.92	39.2	8.74
	♀	50	43	1	3	47	43	.92	37.8	7.28
CS-GL	♂	50	13	2	10	25	13	.52	46.8	11.15
	♀	50	23	2	10	35	23	.66	43.4	11.73
IS-S	♂	50	24	0	9	33	24	.73	12.1	4.93
	♀	50	27	2	11	40	27	.68	13.8	6.85
IS-GL	♂	50	15	2	8	25	14	.56	21.1	15.59
	♀	50	18	3	8	29	18	.62	19.5	15.65

TABLE 2

Partition of Chi Square for Seizure Risk

SOURCE OF VARIATION	*df*	χ^2	*p*
Schedule	1	7.29	.01
Treatment	1	28.09	.001
Sex	1	4.41	.05
Schedule × treatment	1	2.25	NS
Schedule × Sex	1	.01	NS
Treatment × Sex	1	.49	NS
Schedule × Treatment × Sex	1	1.69	NS

was believed that this would reduce seizure incidence in a manner comparable to that of the glutamic acid injections. This prediction was based upon results with a related but different stock of animals. Actually, the reduction in convulsion risk obtained was slightly less than that obtained with glutamic acid (see Table 1).

Design

The experiment was planned so that 50 males and 50 females were tested under each of the following conditions: group CSS—continuous stimulation, saline; group CSGL—continuous stimulation, glutamic acid; group ISS—interrupted stimulation, saline; group ISGL—interrupted stimulation, glutamic acid.

RESULTS

The effects of both glutamic acid and interrupted stimulation are to reduce significantly the seizure risk of both males and females. The data with respect to incidence of convulsions and the number of fatal convulsions are summarized in Table 1. A partition of chi square for seizure risk among each of the three independent variables of the experiment is given in Table 2.

Glutamic acid treatment has the strongest effect on seizure risk, followed by the effect of schedule and of sex. It will be observed that none of the interactions is significant.

It is clear from Table 1 that not only is seizure risk reduced by pretreatment with glutamic acid and by the use of interrupted stimulation, but the severity of convulsions and the death risk are reduced in those animals which do have seizures. With continuous stimulation, glutamic acid reduces the incidence of convulsions 20 per cent more in males than in females (t = 2.06), whereas no sex difference occurs in the saline-treated controls. The reduction produced for each sex below the control level (44 per cent for males, 24 per cent for females) is more highly significant (t = 4.92 for males; 3.12 for females). This is in contrast with the results obtained on repeated injections of glutamic acid, where adaptation occurred in both sexes to the point where no effects were noted on females, and only the incidence of recoveries was changed in males (6, 8). In the present study, both sexes exhibited significant increases in recoveries over the control level (t = 3.86 for males; 2.92 for females). There is a shift in the pattern of the convulsions from the severe clonic-tonic seizure to the clonic seizure and the relatively mild convulsive spasm (see 2).

The increase in recoveries is due entirely to the increase in proportion of milder convulsions in this sample, although in two previous samples an increased proportion of recoveries from clonic-tonic seizures was observed (6, 8). In these cases the seizures are fully as severe as those that terminate fatally in untreated animals, but the mice are able to survive the period of apnea following the convulsions, whereas the untreated mice almost all die as a result of a clonic-tonic seizure unless they are given artificial respiration. All our mice can be resuscitated.

When the interrupted stimulus is used with animals protected by glutamic acid, the results are similar to those obtained with glutamic

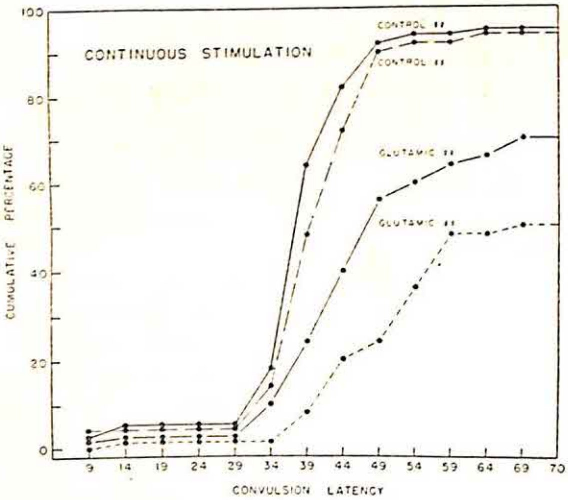

FIG. 1. Convulsion latency of the continuous stimulation groups

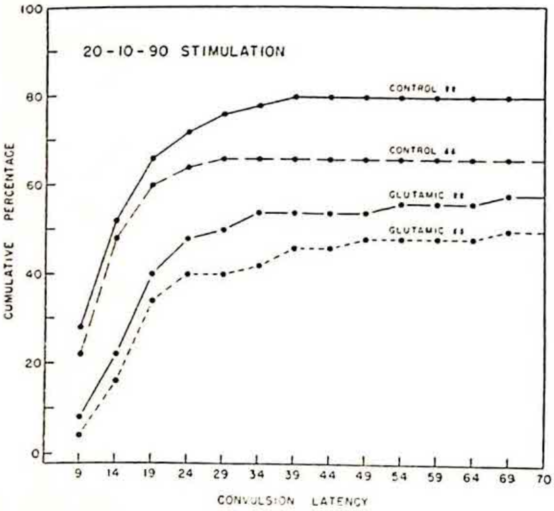

FIG. 2. Convulsion latency of the interrupted stimulation groups

acid on continuous stimulation except that no sex difference appears. The combination of the two protective measures, glutamic acid and interrupted stimulation, on the schedule described, brings the seizure risk in females down to the male level but does not depress the incidence in males below that accomplished by glutamic acid alone.

A comparison between continuous and interrupted stimulation where no glutamic acid is administered to either group reveals that the convulsions have decreased and recoveries increased significantly as a result of interruption, and that all recoveries are attributable to the increase in proportion of clonic seizures and convulsive spasms at the expense of clonic-tonic seizures. The protective effect is considerably less than that achieved with glutamic acid and involves no sex differences that are significant at or below the .05 level of confidence. Whether or not such a sex difference would emerge if the magnitude of the effects achieved with interruption were comparable to that achieved with glutamic pretreatment is not settled by these experiments. Other agents that have given results comparable in magnitude and direction with those obtained with glutamic acid have not necessarily acted differently on the two sexes (6).

The effect of glutamic acid coupled with continuous stimulation on recoveries (expressed as percentage of total) in females is the same as that achieved with saline-injected mice on interrupted stimulation, but the male recovery rate on glutamic-continuous is 16 per cent higher ($p = .0495$).

The results as regards change in the latency of convulsions are shown in Table 1 and in Figures 1 and 2. These accumulative percentage latency diagrams show the marked effect of the change in schedule and of glutamic acid preinjections upon the rate of development of the seizure pattern. A marked difference between these two treatments is found in the latency effect, which is tremendously reduced by prestimulation and increased by glutamic acid, although both experimental groups have a reduced convulsion risk. The differential convulsion risk between the sexes is also shown in the accumulative percentage latency curves, as the female curve always starts to rise slightly ahead of the male curve. The difference is slight, however, and does not reach statistical significance with any of the tests (chi square, analysis of variance) employed. Since it is in the direction which would be predicted from the established relationship between latency and susceptibility, it probably reflects a real difference between the sexes.

The standard deviations of the latencies show a consistent pattern, being greater in all groups receiving glutamic acid. The significance of these differences between saline and glutamic acid pretreatment was determined by the t test (see Table 3).

It may be concluded that one of the effects of glutamic acid is to extend the width of the time band in which seizures may occur.

TABLE 3
Comparison of Saline and Glutamic Acid Pretreatment

GROUPS	t	p
CSGL males—CSS males	1.416	.1
CSGL females—CSS females	2.986	.01
ISGL males—ISS males	5.236	.001
ISGL females—ISS females	4.465	.001

DISCUSSION

The behavioral effects of glutamic acid have been difficult to confirm, let alone quantitate and explain (8). In the present paper previously reported palliative effects of glutamic acid on sound-induced seizures in an inbred strain of mice have been confirmed and extended, but concomitantly, another problem has been raised. It is that the control group (saline-continuous) had a seizure incidence of 94 per cent, some 30 per cent higher than eight previous control samples each of comparable size had given in the hands of a number of different investigators. These latter exhibited remarkable consistency from sample to sample even when bells of different tonal qualities were used and over a range of sound pressures from 86 to 104 db. Although the details of the experiments are not pertinent here, the uncontrolled variable has been identified as prestimulation resulting from the fact that mice in the high-incidence control group reported in the present paper were so placed with respect to the apparatus that they were exposed to repeated sound pressures of 64 db while other mice were being tested. It has been possible to achieve both normal and high-incidence controls by manipulating the intensity and duration of the prestimulation of these mice.[3]

Whether the control incidence is high or normal, the effect of glutamic acid in this strain is to reduce seizure risk, increase recoveries, extend and broaden latencies, and protect differentially in the two sexes. There is a slight difference in response of the two sexes (males more susceptible) in the standard stimulus situation that becomes reliable only when very large numbers are used (8). The sex difference is also revealed in genetic experiments where the results of reciprocal crosses involving DBA/1 are dissimilar (5). Males appear to be most easily affected by mechanical or metabolic intervention. The administration of glutamic acid in repeated-dose experiments protects males but has no comparable effect on females (8). On the single-dose experiments reported here, the effect on males is more profound, and females, too, are protected, but to a lesser degree. Work with other strains (6) has demonstrated that the sex difference in response to seizure-producing stimuli does not exist in all susceptible strains of mice, and that glutamic acid offers negligible protection in some of these strains and does not act differently in the two sexes in every strain where protection occurs. Because the glutamic effect is strain-specific, and because it can be reversed by structural analogues of glutamic acid that compete for the same enzyme systems (1, 6), the protective effect of glutamic acid in DBA/1 mice appears to be due to its ability to counteract a genetically determined metabolic deficiency which, in the untreated animal, results in uncontrolled energy release and motor discharge. In addition, it appears from the fact that untreated DBA/1 mice die in respiratory arrest after a seizure but can be resuscitated, that the anaerobic mechanisms in the respiratory center are deficient, and that glutamic acid compensates for this defect in those treated animals that exhibit clonic-tonic seizures but recover.

The identification of the precise metabolic effects of glutamic acid that are pertinent to these behavioral sequelae has not yet occurred. Waelsch (11) and Weil-Malherbe (12) have recently published comprehensive reviews of the physiological bases for the action of glutamic acid. The interpretation previously offered by Ginsburg, Ross, and co-workers, that the action of glutamic acid stems in large part from its relationship to the tricarboxylic acid cycle, where it may act as a buffer for α-ketoglutaric acid and thereby affect energy transfer mechanisms in the nervous system when a genetic deficiency in these mechanisms exists (8), remains unchanged in the light of new data. Interrupted stimulation on the schedule used in these experiments reduces the seizure risk and increases recoveries among those animals that do convulse. Unlike glutamic, where some 19 per cent of the recoveries are from clonic-tonic seizures, and, therefore, attributable to an effect on the respiratory center, none of the recoveries after interrupted stimulation are from severe convulsions. Increased recoveries by animals receiving continuous stimulation over the controls with interrupted stimulation are wholly due to the increase in the ratio of clonic seizures and convulsive spasms to clonic-tonic seizures, where this is only partly the case with glutamic pretreatment.

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[3] Ginsburg, B. E., & Alexander, P. Unpublished data.

Inspection of the latency figures (Table 1) reveals that when the sexes are lumped, the difference between the corresponding groups on continuous and interrupted stimulation is 25 sec. Empirically, therefore, the 10-sec. period of interruption (after 20 sec. of priming stimulation) achieves half its numerical value so far as its effect on latency is concerned. That 20 sec. of priming followed by 10 sec. of silence cannot be equated to 25 sec. of continuous stimulation in other respects is shown by the fact that the incidence and severity of the seizures obtained with interruption are reduced.

We know from other experiments (3) that if the interval of silence had been 40 sec. rather than 10 sec. long, seizure risk would have fallen to practically zero. It is as though sound prestimulation brought the animal just to the point of convulsion by exciting a nearly critical number of neural circuits. During the period of silence these hyperexcitable circuits one by one become hypoexcitable. When a sufficient number is extinguished, the animal will become refractory; if an intermediate number is extinguished, a milder convulsion will result from the test stimulus. By chance the test latency may even fall in the normal range, but the rate of extinguishing is so rapid that few animals will be caught at this point.

When glutamic pretreatment and interrupted stimulation are combined, the results achieved are identical with those obtained with glutamic acid and continuous stimulation except that the combined effects of these two palliative measures on the incidence of convulsions in females are numerically additive, suggesting that they are independent.

SUMMARY

Glutamic acid pretreatment lowers the susceptibility of DBA/1 weaning-age mice to sound-induced convulsive seizures. This effect is greater in males than in females. Increased recoveries from seizures are due to the fact that more of the seizures are milder, and that the animals are better able to survive periods of anoxia resulting from postconvulsive apnea following a severe seizure.

Interrupted stimulation on the schedule reported lowers seizure incidence. Recoveries are increased solely as a result of a decreased severity of convulsions, and the two sexes are equally affected. The combination of glutamic pretreatment with interrupted stimulation yields results identical with glutamic pretreatment on continuous stimulation in males, but lowers the seizure risk in females by an amount numerically equal to the sum of the protective effects obtained by each of these means separately.

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Received November 23, 1953.

DRIVE REDUCTION VERSUS CONSUMMATORY BEHAVIOR AS DETERMINANTS OF REINFORCEMENT

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In a previous study (4) it was found that a solution of saccharin in water was an effective reward for instrumental learning despite its failure to provide nourishment or reduce hunger (1). The results were interpreted as indicating that elicitation of a strong consummatory response was a more critical feature of rewards than subsequent drive reduction. The purpose of the present research was to examine this interpretation further by comparing the reinforcing value of solutions in which nourishment, sweetness, and prior experience were varied independently. In one experiment, solutions of dextrose were used with and without the addition of saccharin to increase "artificially" the consummatory behavior. In a second experiment, animals were given prior experience with dextrose solutions to permit any reinforcing effects of nourishment to strengthen the consummatory response itself. The measure of strength of the consummatory response in both experiments was amount of solution ingested in 4-min. periods of confinement in a goal box; the measure of strength of the instrumental response was running speed in a runway that led to the goal box.

EXPERIMENT I: REWARD VALUE OF DEXTROSE WITH AND WITHOUT ADDED SACCHARIN

Method

Subjects and apparatus. The *S*s were 24 male albino rats, about 100 days old and of the Sprague-Dawley strain from the Charles River Breeding Laboratories, Brookline, Massachusetts. The basic apparatus consisted of a modification of a 4-ft. runway described in detail elsewhere (5). Its essential features were a starting box with a hinged floor, a runway terminating in a short uphill hurdle, a goal box with a hinged floor, and guillotine doors at each box to prevent retracing. The weight of the animal on the two floors operated microswitches which controlled a Springfield Timer that measured the animal's response time from leaving the starting box to entering the goal box. The end of the goal box had a circular opening 2½ in. in diameter covered with ½-in. mesh cage wire. Through this the drinking tube projected from a 100-cc. graduated cylinder held to the back of the goal box by a broom clip.

Design and procedure. The animals were divided into four groups of six rats and were starved for two days and then adapted for six days to the hunger regime used during training: a daily feeding at noon of 8 gm. (dry weight) of Purina mash. This regime eventually causes weight to stabilize at about three-fourths of normal, and it keeps animals almost maximally hungry around the clock. Water was available at all times from trays in the living cages.

During training the animals were given three spaced runway trials each afternoon for a period of 14 days. On each trial the rat was placed in the starting box, allowed to go down the runway, and confined in the goal box for 4 min. If *S* did not leave the starting box within 120 sec., it was placed in the runway; if *S* did not leave the runway within 120 sec., it was placed in the goal box. The two measures taken were the time to traverse the runway and the cubic centimeters of fluid ingested from the drinking tube during the 4 min. of confinement in the goal box.

The only difference in treatment of the four groups was the nature of the solution available during the 4-min. confinement periods in the goal box during training. These were:

1. Plain tap water
2. A solution of 1.3 gm. of pure saccharin powder per liter of water
3. A solution of 20 gm. of anhydrous dextrose per liter of water
4. A solution of 20 gm. of dextrose plus 1.3 gm. of saccharin per liter of water.

Results

The results of Experiment I are summarized in Table 1, which shows mean runway speed (100 ÷ time in seconds) and amount of reward solution ingested per trial during the last four days (12 trials) of training. All the differences in the table are significant beyond the .05 level except the mean speed for water versus dextrose.

It is obvious in the table that the dextrose solution by itself is a very poor reward compared either with dextrose sweetened with saccharin or with saccharin alone. It is also obvious that mean speed, the measure of strength of the instrumental response, is closely related to mean cubic centimeters in-

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TABLE 1

Mean Instrumental and Consummatory Response Strength during Last 12 Training Trials

Measure	Reward			
	Water (Control)	1.3 gm. Sacc. per Liter	20 gm. Dext. per Liter	20 gm. Dext. 1.3 gm. Sacc. per Liter
Mean speed	5.7	37.7	7.1	58.1
Mean cc. ingested	0.3	4.8	1.9	8.8

gested, the independent measure of consummatory behavior. Thus the sweetest (to humans) solution, the mixture of dextrose and saccharin, elicits the most consummatory behavior and has the greatest reinforcing power. The others are ordered in lesser effectiveness both in stimulating consummatory behavior and in reinforcing the instrumental act.

A possible source of ambiguity in interpreting the data derives from the fact that in the comparison of sweetened and unsweetened dextrose the taste of the reward solution is confounded with the amount consumed and therefore with the amount of nourishment obtained. This difficulty is partly handled by the pure saccharin control group, which did so much better than the unsweetened dextrose group as to leave no doubt that presence of nourishment is not necessary to explain the performance of the group rewarded with the mixture.

The results do not completely answer, however, the question as to whether nourishment helps. It could be argued that without "priming" the dextrose solution with saccharin it never gets consumed in sufficient quantity to reinforce the consummatory response. Once "primed" with saccharin, it then gets consumed in sufficient quantity to reward ingestion and instrumental acts leading to ingestion. This could be used as a drive-reduction explanation of the superiority of saccharin plus dextrose over the saccharin control. The alternative consummatory-response explanation is simply that the mixture is sweeter than the saccharin alone and therefore elicits a stronger consummatory response.

EXPERIMENT II: REWARD VALUE OF DEXTROSE WITH AND WITHOUT PRIOR EXPERIENCE WITH ITS NOURISHING PROPERTIES

Method

Subjects and apparatus. The *S*s were 24 male albino rats from the same source and of the same strain and approximate age as those used in Experiment I. The apparatus was the same as that of Experiment I.

Design and procedure. The animals were divided into four groups of six animals and were given the same two days of starvation and six days of adaptation to the hunger regime as in Experiment I. At the end of the six adaptation days, the animals were given pretraining experience in replicas of the goal box for six successive nights (2:00 P.M. to 10:00 A.M.). Different solutions were available in the drinking tubes in the dummy goal boxes in pretraining as follows: two groups had water only; the other two had 100 cc. of a dextrose solution, the concentration being 20 gm. per liter for one and 26 gm. per liter for the other. The four groups were then given runway training as in Experiment I, the reward solutions for the four pretraining groups being as follows:

1. Pretraining, water only; training solution, 20 gm. dextrose per liter
2. Pretraining, water only; training solution, 26 gm. dextrose per liter
3. Pretraining and training solution, 20 gm. dextrose per liter
4. Pretraining and training solution, 26 gm. dextrose per liter.

It will be noted that because of the pretraining these animals had been on the hunger regime six days longer than Experiment I animals at the start of training.

Experiment II helps to eliminate controversial aspects of Experiment I. Thus Experiment II is essentially an attempt to allow any reinforcing properties of the nourishment in dextrose solutions to strengthen the consummatory response in advance of the use of the solutions as rewards in runway training. Any such learned effects were maximized not only to the taste of the dextrose solutions but also to relevant environmental cues by having the pretraining take place in replicas of the goal boxes used in subsequent runway training.

Results

The pattern of effects of the experimental variables on the consummatory response during training was clear cut. The consummatory response to the 26-gm.-per-liter solution was higher than that to the 20-gm.-per-liter solution and for either solution the effect of dextrose pretraining was a temporary superiority in consumption of training solutions which was overcome by the water pretrained rats in the course of training. The consumption during training is shown in Figure 1, with the data combined first according to pretraining conditions (water

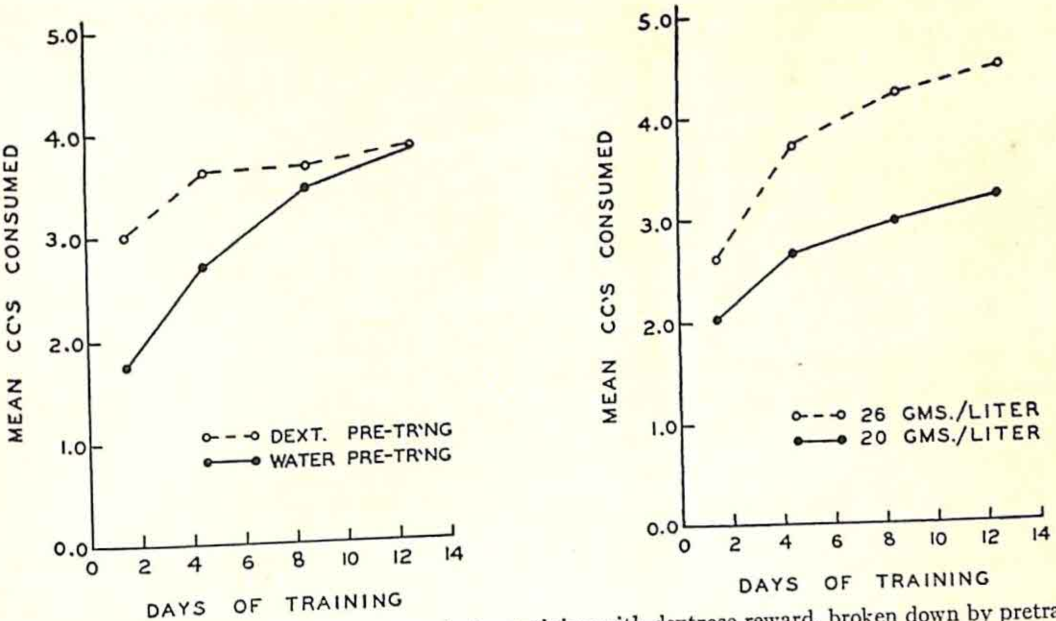

FIG. 1. Strength of consummatory response during training with dextrose reward, broken down by pretraining solution (left graph) and by concentration of dextrose during training (right graph). Data combined for training days 1–2, 3–6, 7–10, and 11–14.

vs. dextrose) and second according to training solutions (20 versus 26 gm. dextrose per liter).

That the pretraining was effective in "priming" the initial consummatory response at the outset of training is apparent in the left-hand portion of Figure 1. Here the animals are grouped into the 12 which had water only and the 12 which had one of the two dextrose solutions during pretraining. The difference in mean cubic centimeters consumed per trial during the first two days of training ($3.03 - 1.78 = 1.25$) has a t of 2.43 (20 *df*) giving a p value of .01 in the expected direction. As training proceeds, however, the water-pretrained animals catch up to the dextrose-pretrained *S*s, and no significant difference remains over the last four days of runway training.

By contrast it can be seen in the right-hand portion of Figure 1 that if the animals are grouped into the 12 which had the 26-gm.–per–liter solution during runway training and the 12 which had the 20-gm.–per–liter solution, the former group starts with a somewhat larger consummatory response and—while both show an increase with training—the initial difference becomes still greater. The difference over the last four days ($4.53 - 3.19 = 1.34$) has a t of 2.26 (20 *df*), giving a p value of .02 in the expected direction.

TABLE 2

Mean Instrumental Response Strength during Last 12 Training Trials (Prior Experience Varied) as Measured by Mean Speed

Pretraining Experience	Training Solution		Difference*
	26 gm. Dext. per Liter	20 gm. Dext. per Liter	
Dextrose-pretrained	37.2	16.8	20.4
Water-pretrained	38.0	21.7	16.3
Difference (dext. − water)†	−0.8	−4.9	

* Over-all mean difference = 18.4; $p = .03$ (both tails).
† Over-all mean difference = −2.8; $p = .70$ (both tails).

Table 2 shows the results for strength of instrumental response during the last four days (12 trials) of training. It is apparent that difference in concentration is the only important factor in this portion of runway performance. Thus mean speed shows no significant difference as a result of prior opportunity to reinforce the consummatory response; what differences were obtained were in the wrong direction. But the more concentrated dextrose solution produced a significantly stronger instrumental response corresponding to the significantly stronger consummatory response seen in the right-hand part of Figure 1.

The results of Experiment II appear to

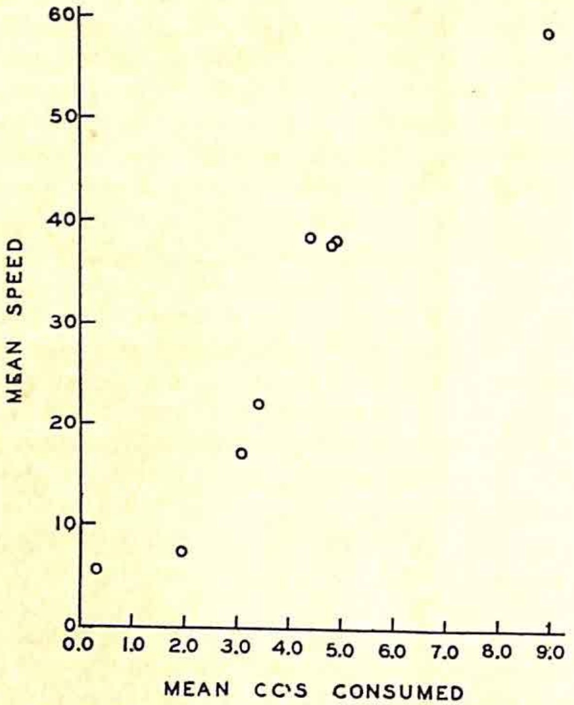

FIG. 2. The relation between the strength of the consummatory response and the strength of the instrumental response with solutions varied independently in sweetness, nourishment, and prior opportunity to practice ingestion. Reading from left to right the groups are: water control, no pretraining; 20 gm. dextrose per liter, no pretraining; 20 gm. dextrose per liter, dextrose-pretrained; 20 gm. dextrose per liter, water-pretrained; 26 gm. dextrose per liter, water-pretrained; 26 gm. dextrose per liter, dextrose-pretrained; 1.30 gm. saccharin per liter, no pretraining; 20 gm. dextrose and 1.30 gm. saccharin per liter, no pretraining.

settle the ambiguities left by Experiment I. If a drive-reduction interpretation were correct, it would be expected that pretraining with nourishing solutions would maximize the strength of the consummatory response so that it would be as well "primed" by pretraining as it was by the flavoring with saccharin in Experiment I. Instead, the outcome was again that the more ingested solution was the more reinforcing, and even *S*s pretrained with the 26-gm.–per–liter solution failed to equal in performance the animals who received the less nourishing but sweeter saccharin and dextrose mixture used in Experiment I. Rather, the animals pretrained with the 26-gm.–per–liter solution in Experiment II achieved an ingestion rate very close to that of the saccharin-only group of Experiment I (over the last four days the mean amount ingested per trial was 4.7 cc. for the former and 4.8 cc. for the latter).

The corresponding mean speeds of *S*s receiving these two rewards, which are about equal in consummatory response but completely different in nourishment, were also close to identical, the nonnourishing, pure saccharin group giving a mean speed of about 38 and the nourishing, pretrained, dextrose group giving a mean speed of about 37. Thus with consummatory response about constant, regardless of nourishment, instrumental performance is about the same.

This rather striking precision in the relationship should be regarded with some reservation since the two experiments were done at different times by different experimenters. It should be noted, however, that the anhydrous dextrose solution of 26 gm. per liter used in Experiment II was selected not only to be more nourishing than the saccharin-plus-dextrose solution of Experiment I but also because an earlier exploratory study using animals having extensive prior experience with dextrose indicated about equal consumption of solutions of 1.30 gm. saccharin per liter and a solution of anhydrous dextrose roughly 20 times as concentrated (i.e., 26 gm. per liter). Thus approximate constancy of the consummatory response with these solutions was anticipated and could be considered part of the experimental design. In a particular experiment, however, it appears that whatever the influences on rate of consumption—substance, concentration, or prior experience—the resultant strength of the consummatory response is a good index of the reinforcing value of the solution in new instrumental learning.

This type of comparison can be made for all eight groups in the two experiments combined. This is shown in Figure 2, where strength of the instrumental response is plotted as a function of strength of the consummatory response, using mean speed and mean amount ingested, respectively, over the last 12 training trials for all *S*s. In view of the fact that the different points represent different solutions, different concentrations, different amounts of nourishment, and different prior experiences, the figure provides a rather convincing demonstration of the degree to which the strength of the consummatory response is related to the strength of the instrumental response without regard to drive-reducing properties of the incentive.

DISCUSSION

The results strengthen the interpretation that the vigor of the consummatory response is the final determining factor in the reinforcing power of a reward for instrumental learning. In the present experiments nourishment per se was apparently irrelevant to learning. Reinforcement was in proportion to calories ingested in the dextrose solutions, but the saccharin controls indicate that this is an artifact of the confounding of calories and sweetness. The position taken here is that sweet stimulation innately elicits ingestion and that this reinforces instrumental learning in proportion to the strength of the ingestion response.

The question may be raised as to why acquisition of dextrose consumption is found during runway training if the consummatory response is innate. In answer to this it should be noted that the presumed innate response is to *sweet stimulation*, and the animal arriving in the goal box must learn to go to the tube and drink rather than investigate during the 4-min confinement period. This shows up as an increasing time at the tube and a corresponding increasing consumption during training. Such acquisition is also found with saccharin, as shown elsewhere (4), and should be regarded as the same sort of process as the acquisition of the runway habit. The innate response can best be observed if the naive hungry animal—while not distracted by the observer—takes a first taste of solution from his living cage water bottle. The consummatory response is immediate and vigorous if the animal is very hungry and the solution is fairly sweet (e.g., 5 to 10 per cent sucrose).

It might be argued that all of the instrumental learning in the present experiments utilized acquired reward based on prior experience with nourishing sweets. This possibility was considered and discounted elsewhere (4), chiefly on the grounds that the reward value of saccharin did not extinguish over long periods of ingesting the solution in distinctive cue contexts. Acquired reward interpretations imply loss of the reinforcing power in the absence of primary reinforcement. The results of Experiment II also fail to support an acquired reward interpretation in that pretraining with sizable amounts of the nourishing solution and in the presence of goal-box cues did not noticeably enhance the reinforcing power of the reward.

The main purpose of Experiment II was to test the possibility that with the dextrose solutions as reward the animals never ingested enough in the goal box to get sufficient drive reduction to constitute an important reinforcement. A small pellet of familiar food makes an excellent reinforcement but is supported by acquired reward from the daily diet. And in Experiment I the innate response to saccharin insured a larger caloric intake per trial than obtained even with the stronger of the two dextrose solutions used in Experiment II. The thought was that if animals had a prior chance to drink large quantities of dextrose, and if nourishment were reinforcing to some extent, the ingestion response would not only strengthen but smaller amounts would take on acquired reward. The Hullian position implies that since faster consumption of a dextrose solution brings greater reward in caloric intake, the hungry animal with sufficient experience should selectively learn to drink as much and as fast as he can, achieving ingestion rates comparable to saccharin-sweetened dextrose.

This latter expectation was not at all borne out with the amount of pretraining used, and the fact that the water pretrained caught up so quickly on consumption during the relatively small exposure to dextrose during runway training argues against the likelihood of insufficient pretraining. In this experiment the asymptotic level of ingestion appears to be a function of concentration independent of nourishing experience.

The present findings are clearly compatible with Thorndike's (6) behavioral definition of a reward as something the animal "does nothing to avoid, often doing something to maintain." They do not lend support to need-reduction or drive-reduction theories (e.g., 2, 3) of the nature of reinforcement, and they raise the question of whether any reinforcement mechanism can be proposed that goes beyond the empirical testing for maintaining or consummatory responses.

To this end it may be noted that in the case of instrumental learning with positive rewards the reward stimulus is at the outset of training an "unconditioned" stimulus for the consummatory response in the sense that it will regularly elicit the response when presented. It would be expected that this terminal consummatory response would become conditioned to immediate neutral cues, especially those which just precede the onset of the reward stimulus. On successive experiences after the first these cues will arouse the consummatory response *ahead* of the reward. Moreover, this arousal of the incomplete consummatory response will work its way from the goal backward over the instrumental sequence since only the cues in this sequence invariably precede reward. Thus performing the correct responses—and only the correct ones—becomes a cue-producing situation that arouses the incomplete consummatory response.

This inference can be made the basis for an explanatory mechanism if one assumes (*a*) that incomplete arousal of the consummatory response produces excitement if the animal is in the appropriate drive state and (*b*) such excitement is channeled into whatever response is being performed at the moment. The first of these assumptions is easy to accept—thus animals on a hunger regime, for example, are practically besides themselves with excitement when exposed to the cues that just precede the arrival of their daily ration in their living cages. If the second assumption corresponds with facts, correct responses would become prepotent over others because they alone would be performed with the added boost of excitement from anticipatory arousal of the consummatory response. And with several incipient response tendencies at a behavioral choice point, the one that arouses the consummatory response would be the most likely to carry through to completion. With training the correct sequence gets the advantage of more rehearsal and more vigorous performance than incorrect sequences.

This alternative to the "drive reduction" mechanism might be called the "drive induction" theory of rewards since it depends on arousal rather than reduction of excitement and treats rewards as incentives rather than satisfiers. It also should be noted that the proposed mechanism requires only a contiguity principle of association.

SUMMARY

1. In the first experiment four groups of six rats each were placed on a hunger regime of 8 gm. (dry weight) of Purina mash per day and were trained in a runway response with the following rewards: (*a*) tap water, (*b*) a solution of 1.3 gm. per liter of pure saccharin, (*c*) a solution of 20 gm. per liter of anhydrous dextrose, and (*d*) a solution of 1.3 gm. of saccharin plus 20 gm. of dextrose per liter. The results were that the saccharin reward reinforced running, but the dextrose was reinforcing only if saccharin was added.

2. In the second experiment four groups of six rats each were placed on the same hunger regime as in the first experiment but were given experience in replicas of the runway goal boxes with either water or dextrose (20 gm. per liter and 26 gm. per liter) available prior to runway training with dextrose. The results were that animals with a previous opportunity to have the consummatory response reinforced by nourishment did no better in runway training than control animals.

3. If runway performance is plotted as a function of the rate of ingestion of the reward solution in the goal box during runway training, for the eight different groups getting solutions that varied in sweetness, nourishment, and previous experience, an almost linear relation is found between strength of the consummatory response and strength of the instrumental response.

4. The results are interpreted as evidence that nourishment per se is an irrelevant aspect of the reinforcing value of sweet solutions in hungry rats and that the strength of the consummatory response determines the reward value of the substance.

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Received January 7, 1954.

REINFORCEMENT OF POSITION PREFERENCE BY AUTOMATIC INTRAVENOUS INJECTIONS OF GLUCOSE[1]

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Whether reduction of physiological need or of drive stimulation (or presentation of associated stimuli) is necessary and sufficient for strengthening a correlated habit (3, 5) has been questioned by recent experimental data. Hungry rats learned to prefer nonnutritive saccharin water to ordinary water (10). The effectiveness of the saccharin persisted longer than secondary reinforcing effects heretofore reported, and has been attributed to the more vigorous consummatory responses elicited by the saccharin (10, 11). Shocked rats learned to prefer stimuli which presumably *increased* fear drive, and the effectiveness of these "dangerous" stimuli has been attributed to their tendency to increase the duration of the (consummatory?) response (2). The present experiment, however, is concerned not with whether need reduction is necessary for learning, but with whether need reduction is sufficient for learning.

Demonstrations of the movement-eliciting properties of the usual sort of reinforcing operations should not lead us to overlook that it might be possible to reinforce a habit by reducing a need in such a way as not to elicit either "consummatory" behavior or secondary reinforcing cues. Introduction of food into the stomach via fistula is reported to have a reinforcing effect (8). The reasonable assumption was made that this method of reducing food need involved fewer consummatory responses of chewing, swallowing, and changing stomach contractility than are involved in eating. The present procedure differs in that by introducing sugar directly into the blood stream there may be: (*a*) even fewer consummatory responses, (*b*) less delay of tissue need reduction, (*c*) greater opportunities for eventually obtaining records of overt and covert consummatory responses, and (*d*) less surgery, less time per animal, and less expense per *S*.

Our working hypothesis is that a hungry rat's preference for a particular head position will be increased by accompanying this position with continuous intravenous injection of glucose solution.

METHOD

Subjects and Apparatus

Subjects for this experiment were 32 male albino rats weighing between 240 and 460 gm.

Apparatus was essentially similar to that employed in previous experiments of secondary reinforcing effects of stimuli associated with onset and with termination of electric shock (1, 2).

Procedure

The procedure began with the deprivation of food for 3 days, following which each rat was restrained in a snugly fitting cage, with head and neck protruding. Under local ethyl chloride anesthetic, the caudal vein was exposed at the base of the tail. A specially prepared 27-gauge needle was inserted proximally and sutured in place. The rat was then placed with its head between vertical beams of infrared light so that horizontal flexion of the head to either side actuated the photoelectric relay on that side.

For a 10-min. period of nonreinforcement, electric clocks totaled the duration of head position left of center and right of center, and operation-recorder pens tallied the frequency of head movements to the left and to the right.

Following this 10-min. period there was a 90-min. reinforcement period during which an average of 4 cc. of liquid was injected. The procedure during this reinforcement period was as follows: First the needle was cleared of any blood clots by momentary pressure from a syringe which was in series with the fluid line. One photoelectric relay was then connected to an electromagnetic valve controlling the flow of fluid from a reservoir 4 ft. above the needle. Fluid could then flow through the valve and into the blood system of the rat as long as the head of the rat was turned toward the nonpreferred side, i.e., the side on which the beam had been interrupted the shorter total time during the 10-min. nonreinforcement period.

Complete chronometer records were obtained from 16 rats reinforced by 10 per cent glucose dissolved in physiological saline and also from 16 rats which were given only the saline solution. Satisfactorily complete

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[1] This research was conducted at the University of Missouri and supported by a grant from the University of Missouri Research Council. Most of the data were presented to Section I of the meeting of the American Association for the Advancement of Science in Philadelphia, 1951.

[2] Now at R. B. Jackson Memorial Laboratory.

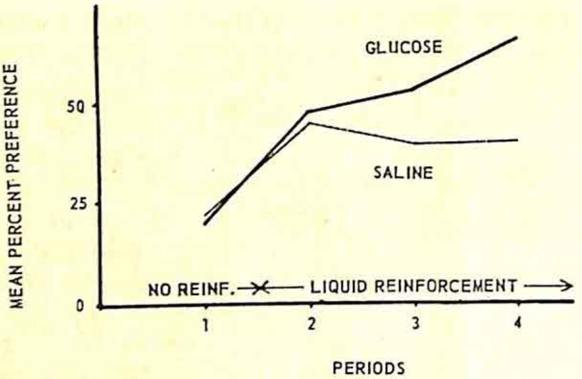

FIG. 1. Effects of correlated injections upon relative preference for a head position

operation-recorder records were obtained from only 14 in each group.

RESULTS AND DISCUSSION

The relative preference of each rat for the reinforced side was determined by calculating the percentage of the total off-center time which it spent on the reinforced side. This preference was determined during the 10-min. nonreinforcement period and the three successive 30-min. periods of reinforcement. The animals injected with glucose learned to keep their heads in the position which kept glucose flowing into their veins (Fig. 1). As in a pilot study involving 15 animals, it took a little while for them to make their choice. However, by the last 30 min. they showed significantly ($p < .01$, Festinger's test) greater preference for the rewarded side than did the saline controls. These results tend to support and extend the findings of other investigators who used fistula feeding (7, 8).

The records from the operation recorder indicated a slight and nonsignificant tendency for an increase in relative frequency of responses toward the reinforced side in the glucose group. Group means of the percentages of total responses which were toward the reinforced side were 32, 41, 48, and 54 during the successive intervals of time. Comparable figures from the saline group were 40, 49, 42, and 45. Significant influences on duration of position but not on frequency of movement toward that position are typical of some experiments in which reinforcing conditions are not discrete but are continued as long as a position is maintained (1, 2).[3]

Significant group differences in measures of *absolute* frequency or duration on the reinforced side were not obtained in the present experiment. It is believed that there is independent evidence that the present apparatus permitted greater unsystematic variation in the following factors than previous apparatus: size and weight of *S*s, alignment of photoelectric cells, and voltage and temperature fluctuations. These factors are controlled, statistically, by using relative preference scores rather than absolute scores.

Mean total activity, i.e., moves toward either side, was 2.6, 3.4, 3.5, and 2.7 responses per minute per glucose-injected rat during the four successive time intervals, and 3.1, 3.1, 2.4, and 3.1 per minute in the saline control group. Additional controls would be necessary to evaluate satiation, revival, response generalization, and other possible factors contributing to total activity.

CONCLUSION

With intravenous injection continuing as long as a rat's head is in a given position, 10 per cent glucose is more effective than saline solution in increasing the relative duration of or preference for that position. The relative frequency of moves toward that position increases, although to a nonsignificant degree. These findings are consistent with the hypothesis that reduction of a physiological need is sufficient for reinforcing a habit.

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Received January 5, 1954.

EQUAL-REINFORCEMENT VALUES FOR SUCROSE AND GLUCOSE SOLUTIONS COMPARED WITH EQUAL-SWEETNESS VALUES[1]

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A previous study of sucrose as a reinforcing agent (4) has shown that the rate of bar pressing of rats under periodic reinforcement is a logarithmic function of the percentage sucrose concentration used as reinforcing agent, over the range of 4 per cent to 32 per cent. On the hypothesis that the reinforcing effects of sapient substances are related to the magnitude of their effects upon taste receptors, it should be possible to predict, for example, the relative reinforcing effects of solutions of two sweet substances if their relative sweetness is known. For humans, isosweetness curves for many nutrient and nonnutrient chemical compounds have been obtained (2), and MacLeod (7) has recently redetermined the sucrose-glucose isosweetness function over the lower portion of the solubility ranges of these substances.

In this study, the reinforcing effects of sucrose and glucose solutions for rats are studied in the aperiodically reinforced bar-pressing situation. For both substances, rate-concentration functions over the range from 2 per cent to 32 per cent are sought in the same group of *S*s. Quantitative predictions concerning the relationships of such rate-concentration functions are based upon two premises: that equally sweet substances used as reinforcing agents will yield equal rates of responding, and that the taste receptors for sweet are very similar in rats and humans. The latter is a tenable assumption on the evidence that rat preference thresholds and human sweet-taste thresholds for sucrose and glucose are comparable (9). These premises jointly lead to the highly specific prediction that if an isosweetness curve is constructed from the rate-concentration curves by selecting pairs of concentration values of the two substances which result in equal rates of responding, the form and constants of such a curve will closely reproduce the curve obtained by psychophysical means.

METHOD

Apparatus

A set of four identically constructed Skinner boxes was used. These boxes and associated recording and control units are very similar to those described by Guttman and Estes (5). The animal is housed in a metal chamber with a transparent roof and a grill floor. This chamber is enclosed in a plywood and Celotex box to provide sound insulation. The animal's compartment is 10 in. long by 8 in. wide by 7¾ in. high. The bar is a rod of $\frac{3}{16}$-in. brass which projects 2 in. into the box through a hole near one side of the front wall and extends along the side wall. The magazine is a solenoid-operated dipper which delivers approximately 0.1 ml. of solution. The dipper opening is at floor level ½ in. in front of the front wall and 2½ in. from the side wall opposite the bar. Bar-pressing responses are recorded by means of a set of graphic cumulative recorders and also by means of magnetic counters. The aperiodic schedule of reinforcements (1-min. mean interreinforcement interval) was provided by a Skinner-Gerbrands punched-film programmer.

Subjects

Eight male white rats bred in the Duke University Medical School colony were used as *S*s. They were 305 to 315 days old at the start of the experiment, and had been used in exploratory studies related to the present experiment. All *S*s were trained to bar press for water under 22-hr. thirst and were given 1100 continuous water reinforcements at ages 107 to 121 days. This was followed by 1 hr. of periodic reinforcement on a 1-min. schedule. All *S*s were then food deprived and water sated and tested under periodic reinforcement with various sucrose and glucose solutions for twelve days. Four *S*s were then used in a series of further exploratory studies in which they were run a total of approximately 87 hr. under periodic and aperiodic reinforcement with sucrose, glucose, or water as reinforcing agents. The other group of four *S*s was not used again until the present study, approximately five months after their initial tests. The four very experienced *S*s will be referred to as the VE group, and the other four as the ME (moderately experienced) group. All *S*s were treated identically in the present experiment.

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[1] This investigation was supported by research grant M-631 from the National Institute of Mental Health of the National Institutes of Health, Public Health Service, and by a grant from the Duke University Research Council.

[2] Acknowledgment is made of the assistance of Maurice Siskel, Jr. in carrying out the pilot studies prior to this experiment and of Mrs. Paula L. Kipnis and Norman J. Wilson in obtaining the data reported here.

Procedure

Each S was given one 50-min. session of aperiodically reinforced bar pressing with each of seven sucrose solutions and seven glucose solutions as reinforcing agents. In addition, each S received two 50-min. sessions with distilled water. For both sucrose and glucose the concentrations used were: 2.0, 3.2, 5.0, 8.0, 12.7, 20.1, and 32.0 per cent by weight. "Percentage by weight" here means:

$$\frac{\text{weight of solute}}{\text{weight of solute} + \text{solvent}} \times 100.$$

This follows the terminology suggested in (8). The sucrose used was Franklin brand commercial granulated cane sugar. The glucose was C.P. d-glucose (Pfanstiehl). Distilled water was used as solvent. On a $\log_{10}$ scale these values are separated by .2 log unit steps. The 16 experimental sessions occurred on successive calendar days, except for session 16 for the VE group, which was run on the seventeenth calendar day.

To determine the order of presentation of solutions, two 8 by 8 orthogonal random latin squares were selected, one for the seven sucrose concentrations, plus water, and one for the seven glucose concentrations, plus water. Animals were assigned to one margin of each square, experimental days to the other margin, and concentrations were substituted for the cell entries. The first day's treatment for four animals was taken from the sucrose square, and for the other four animals from the glucose square. On succeeding days, the Ss alternated between the squares. Two of the VE and two of the ME animals were started on sucrose, and the remaining four on glucose.

During the experiment and for several days preceding, Ss were restricted to 1-hr. eating of dry Purina pellets immediately after the running time. They had free access to water in their home cages.

RESULTS AND DISCUSSION

The empirical rate-concentration curves based on the data for all Ss are shown in Figure 1. It can be seen that rate of responding for sucrose is everywhere above the rate for the corresponding concentration of glucose. This is the general relation which must obtain if the prediction based upon relative sweetness is to hold, since sucrose is sweeter for the human observer.

The rate-concentration curves for the VE and ME groups separately are quite similar to those in Figure 1. The curves for the ME group contain irregularities not present in the data for the VE group, indicating that in this type of experiment the effect of practice is largely to improve the smoothness of the functions.

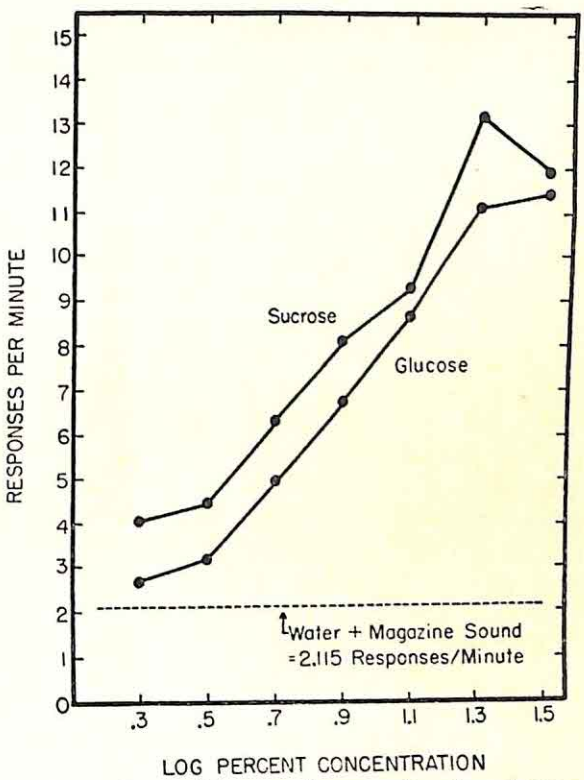

FIG. 1. Rate of bar pressing as a function of concentration of reinforcing agent for all 8 Ss

TABLE 1

Percentage Concentrations of Sucrose and Glucose Judged Equally Sweet by Three Human Ss (MacLeod) and Estimated to Yield Equal Rates of Bar Pressing by Rats

Equal Sweetness		Equal Rates of Bar Pressing	
Sucrose	Glucose	Sucrose	Glucose
1.88	4.24	2.0	4.0*
4.82	7.88	4.8	6.9*
9.18	11.78	9.2	12.0*
21.18	22.05	15.8*	22.0

* Value read second.

The degree of correspondence between the present data and those obtained in human equal-sweetness experiments may be seen in Table 1, where the four pairs of sucrose and glucose concentrations judged equally sweet by MacLeod's three Ss are listed (7). Since MacLeod specified his concentrations in terms of grams of solute in 100 cc. of solution, his percentages have been converted to the present scale by the use of specific gravity tables. For sucrose, the density table in the *Handbook of Chemistry and Physics* (10) was used. For glucose, densities were obtained by means of the formula: $d = 0.99840 + 0.003788p$

$+ 0.00001412p^2$, where d = density, and p = percentage by weight. This function is taken from Bates (1, p. 552). To obtain comparable values from the present rate-concentration data, the empirical (unsmoothed) rate-concentration curves were plotted on large semilog paper which permitted interpolation with an accuracy of .1 per cent for values up to 20 per cent. The first three pairs were read from the sucrose curve across to the glucose curve at given values of rate, and the fourth pair was read in the opposite direction. It can be seen that the present values are a very close match for the first three values reported by MacLeod, whereas the fourth pair does not correspond. The first three pairs are obviously only a sample from an indefinitely large set of comparably good matches which might be drawn from the nearly parallel portions of the rate-concentration curves. Only those portions of the rate-concentration curves which overlap on the rate axis can furnish equal-reinforcement comparisons, but at the upper end of this range, the values are disparate from those of MacLeod.

The lack of correspondence between the present findings and those of MacLeod must be considered in the light of several factors. Where the correspondence is best, between about 2 per cent and 15 per cent sucrose, and about 4 per cent and about 20 per cent glucose, the present data do not differ from MacLeod's by more than the various sets of equal-sweetness results differ among themselves. Above this range, there is diversity of findings among the results on humans. Dahlberg and Penczek (3) and MacLeod report a value of concentration for which the sweetness of the two substances is equal, just below 40 per cent and just below 25 per cent, respectively. On the other hand, Cameron (2) and Lichtenstein (6) present isosweetness curves which indicate no point of convergence of sweetness, and the present results are in qualitative agreement with this alternative. Quantitatively, Cameron's isosweetness relation indicates that 22 per cent glucose is matched by about 17 per cent sucrose (rather than by 21 per cent as found by MacLeod). Although there is agreement between one selected set of sweetness results and the reinforcement results at this point, it must still be borne in mind that comparisons based upon the upper portions of the rate-concentration curves are relatively unsatisfactory and, what is more, tenuous, since there are indications that the upper portions of these curves are probably relatively unreliable compared with their more linear middle portions. The previous study on sucrose cited above (4) yielded a monotonic, relatively linear rate-concentration function up to 32 per cent, and in all the present pilot studies, both sucrose and glucose functions were monotonic up to 40 per cent. In effect, questions of reliability of both sets of data preclude for the present any final statement regarding the confirmation of the experimental hypothesis for higher concentration values.

A point of interest concerns the reinforcement thresholds for sucrose and glucose. The reinforcement threshold has been defined (4) as that value of reinforcing stimulation which will produce conditioned response strength just in excess of the unconditioned strength of that response. In the present instance, reinforcement thresholds might be estimated by extrapolating the rate-concentration functions toward the origin and finding their respective intercepts with the base line established by the background stimulation provided by water and the operation of the magazine. Since the present curves are not linear, such extrapolations have not been attempted, but it can nonetheless be seen that the reinforcement threshold for sucrose is probably lower than that for glucose. This is consistent with the relation between the absolute sensory thresholds for these substances in humans. Moreover, it is not incautious to suggest that the values of the absolute limens (about .5 per cent for sucrose, and about 1 per cent for glucose) would provide approximately correct intercepts for the present rate-concentration curves on the water + magazine sound base line (Fig. 1).

SUMMARY AND CONCLUSIONS

An attempt was made to see whether the relative reinforcing values of sucrose and glucose solutions for rats in the aperiodically reinforced bar-pressing situation are consistent with the relative sweetness of various concentrations of sucrose and glucose for human observers. Four very experienced and four moderately experienced rats were given one

50-min. test on each of seven sucrose and seven glucose concentrations, plus two tests with water reinforcement. Rate of bar pressing was found to be an increasing function of concentration of both substances, with the rate for sucrose always above that for glucose at a given concentration. Between about 2 per cent and 15 per cent sucrose, and between about 4 per cent and 20 per cent glucose, the pairs of concentrations which yield equal rates of responding are in close agreement with the pairs judged equally sweet by human *S*s. Above these ranges, the correspondence is relatively inexact. The findings are considered compatible with the theoretical expectation that the effects of reinforcing stimuli upon receptors are closely related to their reinforcing properties.

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Received March 29, 1954.
Early publication.

ACTIVITY AS A FUNCTION OF A RESTRICTED FEEDING SCHEDULE

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A previous study (3) indicated that when albino rats were placed on a feeding schedule of 23-hr. deprivation and 1-hr. feeding, their activity increased as a negatively accelerated function of the number of days of restricted feeding. This was in sharp contrast to the relatively constant level of activity for control animals on an ad libitum feeding schedule. These findings would seem to question the implicit assumption found in many learning experiments that equal, daily periods of deprivation do not result in any systematic change in strength of drive.

One possible defect of the previous study, however, was that the data were obtained from animals which had been deafened. Although this was done to prevent any social facilitating effect which the noise of the turning wheels might have had upon the activity of the animals, it is conceivable that the surgical techniques utilized in the deafening process or the resultant sensory deprivation might have contributed to the experimental findings. Thus, generalization to normal animals becomes somewhat tenuous. It was the purpose of the present study to replicate the previous study utilizing nondeafened animals.

It would also seem that this study, as well as the previous one mentioned (3), has relevance to a recent study by Campbell and Sheffield (1). These authors have challenged the commonly held assumption that "increased 'drive' produces increased random activity." Their hypothesis is that "drives involve lowered thresholds to external stimulation," and from this they predict there should be "little change in activity in an animal in a drive state unless there were some external stimulation." They dismissed those studies which had previously indicated a functional relationship between strength of drive and activity (5, 6) by pointing out that no specific attempts were made in those studies to maintain a constant environment.

METHOD

Subjects

The *S*s were 20 male albino rats, aged 90 to 100 days at the beginning of the experiment, obtained from the animal colony of the Pennsylvania State University. Three animals from the experimental group and one from the controls died during the course of the experiment.[1] As a result, the final N was 16, which consisted of 7 experimental and 9 control animals.

Apparatus and Procedure

Only a brief outline of the procedure will be presented inasmuch as it has been described previously (3). The number of activity wheels (ten) necessitated the running of the study in two consecutive sessions in order to provide a suitable N. The apparatus consisted of ten standard Wahmann activity drums equated for frictional torque by the method of Lacey (4). The drums were located in a light-tight room and upon a macadamized floor. Room temperature throughout the experimental period was recorded continuously with a thermograph. The temperature averaged 72° with a range of 65° to 75°. Daily fluctuations rarely exceeded 2°.

The animals were first randomly assigned to the experimental or control group and then placed in the wheels; each session originated with five experimental and five control animals. The animals were then given an *adaptation period* of 14 days. Food and water were continuously available during this period. Immediately following the adaptation peroid, the *base period* began. This consisted of a seven-day period in which the room was isolated and darkened except for a daily 1½-hr. period under full illumination (10:30 A.M. until 12:00 M.). During this time counter readings were taken, the animals weighed, and food and water replenished. Food and water were continuously available during the base period. The *experimental period* immediately followed the base period and continued for 21 days. The control animals continued on the base period regimen. The experimental animals were placed on a restricted feeding schedule and permitted access to food only from 11 A.M. until 12 M. each day. Water was continuously available during this period.

RESULTS AND DISCUSSION

Each animal's base rate (in revolutions per day) was obtained by totaling the number of recorded revolutions during the seven-day base period and dividing by seven. The animal's activity for each experimental day was

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[1] An incidental and somewhat puzzling finding has to do with the deaths occurring in the experimental group. It seems unusual to have 30 per cent of the experimental population die during the course of an experiment. Two previous studies (3) show similar findings, however. The behavior of these animals, until approximately three days prior to their death, followed the general rise in activity of the normal experimental animals. At this time, their activity level increased markedly and continued on a high level until death.

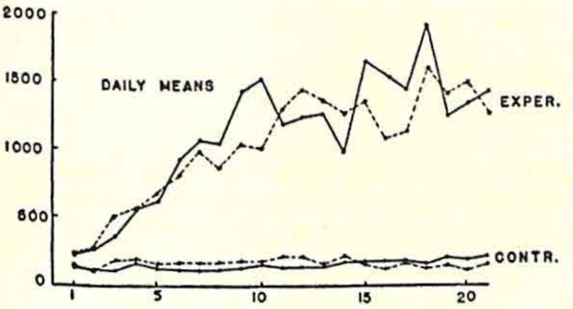

FIG. 1. Mean daily running activity, in percentage of base rate. Broken curve, Exp. II (3); solid curve, present experiment.

divided by the base rate in order to obtain a daily figure expressed in terms of a percentage of the base rate.

The large difference between the variances of the experimental and control groups necessitated the use of the Festinger technique (2) to test for differences in activity. Each animal's daily running activity, in percentage of base rate, was totaled and a mean obtained for the 21-day period. Appropriate rankings based on these means were then given to the experimental and control animals. Results indicated that the difference between the experimental and control groups was significant beyond the .01 level of confidence.

The means for the experimental and control animals for each day of the experimental period are indicated in Figure 1, along with the means of the previous study (Exp. II, 3) which utilized deafened animals. Statistical analysis, as well as inspection of these curves, supports the position that the deafening procedure and subsequent sensory deprivation did not result in the production of significant differences between the two experimental or the two control groups.

The results tend to extend and lend further support to the previous findings that a restricted feeding schedule results in increased activity, and presumably increased drive strength. It is difficult to reconcile these findings with the hypothesis proposed by Campbell and Sheffield (1). It will be recalled that these authors stated there should be "little change in activity in an animal in a drive state unless there were some external stimulation." Constant external environments were present and yet significant differences in activity were produced as a function of different drive strengths. Furthermore, it would seem that the Campbell-Sheffield hypothesis would predict that the decreased external stimulation for the deafened animals would result in a lowering of their activity as contrasted with the normal animals. This is not supported either in the experimental or control groups. It is possible that the exceedingly short interval of time that activity was recorded (10 min. per day for seven days) has resulted in their particular findings, or that the effect of auditory stimulation on activity is different from that of visual stimulation. If the latter is true, the generality of the Campbell-Sheffield hypothesis would seem to be considerably restricted.

SUMMARY

The present study was an attempt to determine the activity level of nondeafened albino rats placed on a restricted feeding schedule. Nine control animals were given free access to food and water; seven experimental animals were given free access to water but had 23-hr. daily food deprivation. The activity of the control group remained relatively stable, but the mean daily activity of the experimental group increased markedly. These findings showed marked similarity to a previous study which had used deafened animals. The results extend the findings of the previous study as well as question a recent theory of drive proposed by Campbell and Sheffield.

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Received February 22, 1954.

REINFORCEMENT VS. CONSISTENCY OF EFFECT IN HABIT MODIFICATION[1]

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When one attempts to train an animal to make a second response to a situation after it has already acquired an initial response, a factor not present in the initial learning must be considered. This is the interference of the previous learning with subsequent learning. When two situations demand different responses, the interference is at a minimum, but when one keeps the perceptual situation the same and wishes to substitute one response for another, the interference is maximum. What is the nature of the interference? One view, expressed by Spence (6), states that a second habit will supersede a first one when the second has been made the stronger of the two. According to this view the first habit would be replaced rather than destroyed by this subsequent learning. Reversing the process again would be a matter of further altering relative excitatory values.

Another view would be to consider the replacement a two-step problem, one being the destruction or the avoidance of the first habit, the other being the building of the second habit. Viewed as a two-step phenomenon, certain motivational and perceptual complications present themselves. One of these has to do with the way an animal's expectations are related to consequences.

The present experiment is an attempt to explain the problem of learning when one response is replaced by another, and in particular, to determine whether the concept of reinforcement is adequate for accounting for the acquisition of learning that is in conflict with previous training.

It readily becomes apparent that if animals have learned a first response, an attempt to alter this response may still lead to partial reinforcement. For example, if one wishes to change a discrimination response from a spatial to a nonspatial one, animals will still be rewarded for the spatial responses every time the positive card is on the side of the spatial response. Although the animal will be punished just as often as it is rewarded, it is not safe to assume that these two effects will neutralize each other.

In order to explore this problem we may introduce different ratios of reward and punishment for practicing the old response. From a reinforcement viewpoint reward-punishment ratios of 80:20 and 20:80 differ more from each other than either differs from a 50:50 ratio; but from the viewpoint of consistency of effect the extreme ratios are more like each other than either is like the 50:50 ratio. The notion of consistency of effect assumes that learning depends upon the ease with which an animal can learn what leads to what. The two extreme ratios lead to the same thing (reward or punishment) on 80 per cent of the trials, but the 50:50 ratio is as inconsistent as possible. The reinforcement viewpoint emphasizes the nature of the effect and makes the degree of consistency secondary.

METHOD

Subjects

Forty-nine animals were used in this study. They were taken from the stock maintained in our laboratory and were between 120 and 180 days old at the beginning of the preliminary training period. These were divided into three groups. Group A contained 15 rats; group B, 20 rats; and group C, 14 rats. A split-litter technique was used to divide them into the three groups. In order to make group B somewhat larger (to allow another subdivision) than the other two groups six of the seven animals remaining were placed in group B and 1 in group A.

Apparatus

A modified Lashley jumping discrimination apparatus was used (1, 2). Two stimulus cards were employed throughout the experiment: one contained a white circle on a black background, the other a black circle on a white background.

Procedure

Preliminary training for all animals. The taming of rats and the methods for training them to jump at cards were standard (1, 2, 5, 6). In all phases of this preliminary training, the animals received ten trials per day. If an animal showed a preference for either of the cards or sides, it was guided with the hand and

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[1] This study was aided by a grant to the senior author from the Horace H. Rackham School of Graduate Studies.

forced to jump to the alternate side or card. The stimulus cards were moved from side to side in a prearranged random order so that all animals experienced jumping to both cards and to both windows an equal number of times.

Training of initial position habit. In establishing position responses in all of the animals, the method of changing stimulus cards from side to side was continued, but whichever card happened to be placed on one of the sides (right or left) was consistently locked, whereas the card placed in the opposite window was always unlocked. When the unlocked window was chosen, the card fell over and admitted the rat to the feeding platform, but when the locked window was chosen, the rat received a bump on the nose and fell into a net 2 ft. below. The side rewarded was the one the animal jumped to on the first experimental trial (both windows were unlocked). This training was continued for 16 days with ten trials a day.

Training on discrimination habit. This is the crucial part of the experiment. All animals were required to give up their position habits and to adopt a discrimination response. The card containing the white circle on the black background was made the positive stimulus, and the card containing the black circle on the white background was made the negative stimulus.

Three methods for changing the spatial to the nonspatial habit were utilized. Each of groups A, B, and C was trained by the method given the same designation.

Method A was designed to set up a reward-punishment ratio of 80:20 for practicing the previously learned position response and at the same time to offer consistent reward for the new discrimination response. In order to accomplish this, the positive card was placed on the side of the animal's position habit on eight out of ten trials given daily and on the side opposite the position habit on the other two trials (the fifth and the tenth). As a result, an animal that expressed its position response was rewarded eight times and punished two times on each day.

Method B was designed to set up a reward-punishment ratio of 50:50 for the position response and to offer reward for all correct responses. Accordingly, the positive card was placed on the side of the animal's position habit on five out of ten trials, and on the opposite side on the other five trials. In this instance, animals practicing the old position habit were rewarded five times and punished five times on each day. Two variations of the 50:50 reward-punishment ratio were used. For half the animals the negative and positive cards were on the "position" side on alternate trials; for the other half the positive card was on the "position" side for the first five trials of a day and on the opposite side for the last five trials.

Method C was like *Method A* except that the positive card was on the "position" side on two trials per day (the fifth and the tenth) and on the opposite side on eight trials. This, of course, resulted in rewarding a position response twice and punishing it eight times daily.

Twenty days of ten trials per day were allowed for changing the position habit to the discrimination response. Our previous research (4) has shown that if the animals are unable to abandon their position habits within this period, they rarely do so with hundreds of additional trials.

TABLE 1

Acquisition of Position Habit

Group	No. of Animals	Response Learned		Average No. Trials Response Practiced	Per Cent of Total Trials
		Right	Left		
A	15	7	8	159.3	99.5
B	20	4	16	159.7	99.8
C	14	8	6	159.1	99.4

Rats that never once deviated from their position responses were classified as fixated. The criterion for abandoning the position response was a single exception to a strict position response. This criterion is more meaningful in practice than it appears at first glance. An animal that violates its position response continues this for a period and then either learns the new response or reverts to a position response (sometimes the old one, sometimes the opposite). The criterion for learning the required response was 30 consecutive errorless trials.

RESULTS

Formation of the Position Habit

Table 1 shows the breakdown of the data in terms of the groups. At this stage of training, all groups were treated alike, so the similarities obtained are to be expected. We do not know why group B developed more left-going position habits than groups A and C.

The fact that there was such a rapid acquisition of the position habits in all groups suggests that the response chosen on the first experimental trial corresponded with the natural preference of the animals. The *position habits* formed by rewarding the responses chosen on the first trial should not be confused with *position stereotypes* formed in an insoluble problem situation (4).

Modification of the Position Habit

Table 2 presents the data on the modification of the position habit by the three different reward-punishment ratios in terms of the number of rats persisting in the position habit (i.e., developing fixations) and the number able to change. Two measures or criteria of change are used: (*a*) the proportion that gave up their position habits, and (*b*) the proportion that adopted the discrimination response. The second criterion is more strict than the first since an animal might give up a position re-

TABLE 2

The Influence of Three Reward-Punishment Ratios on the Modification of Behavior

Reward-Punishment Ratio	No. of Rats Persisting in Position Habit	No. of Rats Abandoning Position Habit but Not Learning	No. of Rats Learning Discrimination Response
Method A (80:20)	6 (40.0%)	2 (13.3%)	7 (46.7%)
Method B (50:50)	14 (70.0%)	2 (10.0%)	4 (20.0%)
Method C (20:80)	4 (28.5%)	4 (28.6%)	6 (42.9%)

sponse and still not learn the discrimination response.

General inspection of the table reveals that no method of training was successful in causing all animals to abandon the position response. However, the proportion of animals that persisted in their position responses (i.e., fixated) did vary. It is clear that a linear trend demanded by reinforcement concepts does not occur. Rather, Method B produced a greater proportion of fixations than either of the extreme conditions. If we combine the data of Methods A and C, we find the number of fixations to be significantly less than the number obtained with Method B (chi square with 1 *df* and corrected for continuity equals 7.72, which is significant at the 1 per cent level).

A similar picture is obtained if we use the more strict criterion: the number of animals that actually learned the discrimination response under the three methods. The last column of Table 2 shows the percentage of learners with Method B to be less than half as large as with the other methods. If the results of Methods A and C are combined, the results differ significantly from those of Method B (chi square of 5.91, significant at the 2 per cent level).

Let us next examine the learning scores of the animals that learned the discrimination response. Table 3 presents the data on the number of trials required for the abandoning of the position response (lenient criterion) as well as the number of trials required for the acquisition of the discrimination habit (strict criterion). It should be noted that we are dealing only with the rats not persisting in their position responses.

TABLE 3

Analysis of Learning Produced by Varying Reward-Punishment Ratio

Reward-Punishment Ratio	Average No. of Trials (First Violation) to Abandon Position Response	Average No. of Trials to Learn Discrimination Exclusive of 30 Criterion Trials
Method A (80:20)	90.4	114.3 (80–140)
Method B (50:50)	58.3	90.0 (70–110)
Method C (20:80)	28.0	101.6 (30–150)

The second column of Table 3 presents the average number of trials required for abandoning (first violation) the position response. In this instance Method C is best and Method A is poorest. The difference between Method A and Method C yields a t value of 5.33 which for 17 *df* is significant at the 1 per cent level. The differences between Methods A and B (13 *df*) and between Methods B and C (14 *df*) yield t values of 2.03 and 2.13, respectively. These values are significant at the 5 per cent level. It is clear that the rate of abandoning a position habit is directly related to the frequency with which the position habit was punished. Here a linear relationship holds as reinforcement concepts demand. However, this effect does not apply to all rats, only to those that did not fixate.

When the number of trials required for learning the discrimination habit is considered, a different trend occurs. On the basis of this criterion Method B is best and Methods A and C approach each other. The third column shows the averages and the ranges in these measures.

The most significant difference between the groups is the difference between Methods A and B, and this difference is significant at the 5 per cent level ($t = 2.11$). Since the trend is opposite to that obtained when the percentage of learners is used as a criterion, it is clear that a possible difference in the difficulty of the learning problem confronting each group is excluded. The trend in the data also is in opposition to an interpretation in terms of reinforcement.

Another measure of learning available in this study is the appearance of differential abortive behavior (2, 4, 5). Animals soon learn to protect themselves in jumping to the cards

TABLE 4
Frequency of Differential Abortive Jumping

Method	Number of Rats	Per Cent Showing Differential Abortive Jumps	Average Day Differential Abortive Jumps Appeared
A	15	33.3	8.6
B	20	70.0	6.1
C	14	71.5	6.8

by striking the cards with the sides of their bodies rather than their noses. When they jump abortively more often to the negative than to the positive card, they are expressing a discrimination between the cards.

Table 4 shows the number of animals that expressed their discrimination learning in this manner. It is apparent that in this instance Method A is the poorest training procedure and that Methods B and C are approximately equal. (The biggest difference is significant at the 6 per cent level, so these data should be considered as suggestive only.)

Since Methods B and C produced similar results in the abortive jumping, it seems reasonable to suppose that abortive jumping is the animal's simple defense against punishment. When punishment is fairly frequent, it comes to expression, but when it is rare, as in the case of Method A, most animals are not motivated to express their learning by jumping abortively.

Finally, the nature of the results obtained with the two variations of Method B should be considered. The purpose of these two variations was to determine whether or not the frequency with which a card was changed in a window influenced the degree to which its properties would be noticed.

No differences were obtained between the two variations with respect to the number of animals (*a*) persisting (seven for each variation), (*b*) abandoning position responses but not learning (one for each variation), or (*c*) learning the discrimination habit (two for each variation).

It follows that if making one exchange of the cards in a window produces the same results as making nine exchanges, the frequency of exchanges had no bearing on our results. Thus Methods A and C, which had three exchanges each, did not produce results different from Method B because the stimulus cards were exchanged between windows more or less often.

DISCUSSION

In evaluating the effectiveness of three reward-punishment patterns in causing rats to change their spatial to nonspatial habits, the following six measures of learning were used: (*a*) the number of animals persisting in their initial responses, (*b*) number of animals adopting the second response, (*c*) the number of trials required to give up the first response, (*d*) the number of trials required to adopt the second response, (*e*) the number of animals showing differential abortive jumping, and (*f*) the number of trials required to develop differential abortive jumping. In only one of these measures was the linear relationship demanded by pure reinforcement obtained.

This measure demonstrated that, among animals that learn, the speed with which they abandon a response varies directly with the proportion of punishment (see Table 3). However, even among these animals that learned, there was no indication that the acquisition of the new response was aided by the rapid abandonment of the old one. Therefore, the time gained in getting an animal to abandon an old response was not successfully used in developing a new response. This makes one question whether or not the reinforcement pattern was conducive to learning after all.

Far more important in determining the behavior of animals in this study was a perceptual factor. When the reward-punishment pattern was either 80:20 or 20:80, significantly more animals gave up their old habits than when the reward-punishment pattern was 50:50. The 80:20 and the 20:80 patterns are cognitively alike in that whatever happens in connection with a choice the animal makes happens with the same degree of regularity. To be accurate one should say that regularity is more important to learning than the difference between reward and punishment.

This does not mean that reward and punishment have an equal effect on the animal. Rather, their similar effect is on the animal's learning. Once an animal has learned, it uses this learning to satisfy needs. A rat expresses its preference and makes choices, but these are problems in motivation. In the present experiment the animals avoided punishment by abandoning the position habit the most quickly by the method that gave punishment most frequently. This does not mean they learned more quickly, but the need to do something about what they knew was more urgent. Under the most punished condition, the animals that learned avoided the position response after an average of 28 trials, but they did not solve the problem until 101.6 trials had elapsed (an interval of 73.6 trials). Under the least punished condition the position response was not avoided until an average of 90.4 trials had elapsed and then the problem was solved after 114.3 trials (an interval of 23.9 trials). Is it not more reasonable to interpret these data in terms of the needs to act in certain ways than in terms of the amount of knowledge acquired?

Another manner in which the animals expressed their dislike of punishment was by their attempts to avoid it. Abortive behavior (striking the card with the side of the body) is the most common method used by rats. Abortive jumping was least pronounced under Method A where punishment was minimum, but it was about equally frequent for Methods B and C where punishment was given on 50 and 80 per cent of the trials, respectively.

But why did not abortive behavior continue to increase as punishment increased from 50 to 80 per cent? It may be that 50 per cent punishment is frequent enough to produce maximum motivation or that Method B is best for learning (as shown in Tables 3 and 5) and Method C is most motivating for abortive jumping. Since each has one of these two advantages over Method A, both produce more frequent differential abortive behavior than Method A.

This analysis of the way the rats responded to the problem situation applies only to those which did not become frustrated. The frustration-fixation hypothesis (4) seems needed to account for the failures to give up the position habit in all the groups. According to this view each animal has a frustration threshold. When frustration occurs, problem-solving behavior is replaced by fixated behavior. Method B appeared to frustrate more animals than the other two methods, and at the same time it was most conducive to rapid learning. A similar condition has been described previously (2, 4, 5) and was partly responsible for defining frustration in terms of the animal's physiological condition.

This experiment does not give a clear-cut picture of all the factors that operate when a rat changes its behavior from a position response to a discrimination response. However, one thing seems clear: the modification of behavior is not merely a study of reinforcement increments. If it were, the conclusion as to which of the three reward-punishment patterns tested was best would depend upon which of the several criteria used to measure change was selected. However, if we consider motivation, perception, and learning to be independent variables, all of which influence performance, the data do not appear self-contradictory. It is possible therefore for: (*a*) some rats to fail to show abortive jumping when punishment is infrequent even when they have learned the discrimination (see Tables 2 and 4); (*b*) frequent punishment to make for the giving-up of an old response long before a new one has been learned (see Table 3); and (*c*) rats to continue a position response even after a card response has been learned (see Tables 2 and 4).

The weakness of pure reinforcement theory is that it combines motivation, association formation, and perception into a single concept. In order to make this oversimplified concept fit data at all, it has been necessary to oversimplify learning problems. In being overanxious to find a general principle that would incorporate several others, we may have closed the door to the full exploration of an organism's behavior potentialities.

SUMMARY

Position habits in a Lashley discrimination apparatus were developed in a total of 49 rats. Although different stimulus cards were placed in the windows, each of them was rewarded randomly. When position habits were practiced for approximately 160 trials, the animals were required to learn to respond to a *particular* card, regardless of the side that it was on. Thus the animals had to change a spatial habit to a nonspatial one.

Three methods for changing the response were used. These methods varied the propor-

tion of trials that the old response was rewarded and punished. In each instance, however, the correct response was rewarded on every trial that it was practiced.

The reward-punishment ratios used were as follows: Method A, 80:20; Method B, 50:50; and Method C, 20:80.

Various criteria of measuring the relative superiority of the three methods were used. The results obtained are as follows:

1. None of the methods caused all the rats to give up their old responses.
2. In terms of the number of rats giving up the old response and the number learning the new, Methods A and C are about equal and together they are significantly superior to Method B.
3. In terms of the number of trials required by the learners to give up the old response, Method C is best and Method A is poorest.
4. In terms of the number of trials required by the learners to adopt the new response, Method B is best and Method A is poorest.
5. In terms of the number of animals showing differential abortive jumping, Methods B and C are equal and superior to Method A.
6. In terms of the average number of days required for abortive jumping to appear, Method B is best and Method A is poorest.

From the point of view of reinforcement theory, these data are contradictory, and only the third point supports the concept. A perceptual factor, which we called *consistency of effect*, seems to be more important and basic for explaining the results. According to this concept reward-punishment patterns of 80:20 and 20:80 are alike—only the type of effect differs. However, motivational concepts, frustration threshold, and association formation all played a part in the interpretation of the data.

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Received June 13, 1953.

THE ACQUIRED REWARD VALUE OF AN INTERMITTENTLY PRESENTED NEUTRAL STIMULUS[1]

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The concept of secondary reinforcement has become an important aspect of psychological experimentation and theorizing within the past few years. It has been demonstrated in a variety of situations employing several classes of organisms.

The usual definition of secondary reinforcement states that previously neutral stimuli which are associated repeatedly and consistently with a reinforcing state of affairs will eventually become reinforcing themselves. This is the definition to which Hull subscribed, and its formulation in this manner is generally attributed to him. In a recent presentation of his system he defined secondary reinforcement in this manner: "A neutral receptor impulse which occurs repeatedly and consistently in close conjunction with a reinforcing state of affairs, whether primary or secondary, will itself acquire the power of acting as a reinforcing agent" (5, p. 28).

Many experiments have indicated that secondary reinforcement is capable of influencing the behavior of the rat. Two early experiments were those of Skinner (13) and Bugelski (2). Many others may be cited. A list of studies dealing with a demonstration of secondary reinforcement can be found in Miller (8).

Secondary reinforcement has received attention in theory, too. Spence (14) has suggested that it accounts for all learning under conditions in which delay of primary reinforcement occurs. Hull (5) has utilized secondary reinforcement as an important corollary in his system, and Seward (11) has employed the concept in his theoretical formulations.

In addition to experiments which aimed at a demonstration of secondary reinforcement, there are several recent experiments which were designed to offer a more specific definition of the principle by investigating some of the conditions deemed necessary for its development. These investigations (1, 6, 10) were directed toward a determination of the influence of temporal factors in the development of secondary reinforcement.

One aspect of the definition has apparently not been studied, and its investigation was undertaken here. The definition is not explicit with respect to what is involved in presenting a neutral stimulus repeatedly and consistently. If it is assumed that *repeated* and *consistent* can be varied independently, the role of each factor in the development of secondary reinforcement can be subjected to study. In the present experiment, the repetition of the neutral stimulus was varied while the consistency (i.e., duration, intensity, and temporal distance of the stimulus from reinforcement) was held constant. Specifically, the experiment was an attempt to determine whether a neutral stimulus intermittently presented with primary reinforcement could become a secondary reinforcer.

METHOD

Subjects

Sixty naive female hooded rats were employed in the experiment. They were obtained from the animal laboratory maintained by the University of California at Los Angeles. On the first day of training they ranged in age from 77 to 119 days; the average age was 94 days.

Apparatus

A modified Skinner box constructed of 1-in. pine wood was employed. The inside dimensions of the box were 10 by 10 by 12 in. On one side of the box a brass rod ¼-in. in diameter projected into the box a distance of 1 in. Its resting position was 3 in. from the floor of the box. A small metal food tray was located at the base of the opposite wall. A plastic tube was inserted in an opening ½ in. in diameter 1 in. above the tray, and this permitted the introduction of food pellets. The inside of the box was painted dull gray.

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[1] This paper is part of a dissertation submitted to the Department of Psychology, University of California at Los Angeles, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The author wishes to express appreciation to Dr. Irving Maltzman for helpful suggestions in planning and executing the experiment.

[2] Now at the Primate Laboratory, University of Texas.

The presence of the neutral stimulus, a buzzer, was controlled by *E*. When the buzzer switch was closed, a bar response caused the buzzer to sound. When the switch was open, a bar response did not cause the buzzer to sound. A bar depression activated a condenser timer-relay circuit, and if the buzzer switch was closed, the buzzer sounded for 1 sec. A weight of 12 gm. was necessary to close the circuit. When the procedure called for absence of the buzzer, a small light connected into the circuit informed *E* when an adequate response had been made.

Procedure

A period of five days was allotted for the development of a 24-hr. hunger rhythm prior to the time *S*s were required to press the bar for food. On each of the first three days of this period all *S*s were permitted access to food in their home cages for 1 hr. This feeding rhythm was maintained throughout the entire experiment. The diet consisted of small pellets of dog food.

On the fourth and fifth day, *S*s were placed in the apparatus in groups of 3, 4, or 5 and allowed to eat for 5 min. The bar was not present. On the fifth day, after *S* had eaten in the box in a group, it was again placed in the box, this time by itself. It was now allowed to eat 10 pellets dropped down the chute. The pellets were dropped one at a time at approximately 1-min. intervals. When all pellets had been consumed, *S* was placed in an individual feeding cage.

Training to bar. Training with the bar present began on the next day. The *S*s were required to press the bar in order to obtain a pellet of food. Each *S* received ten trials per day for four days. Those *S*s that failed to press the bar ten times within a 20-min. period on either the third or fourth day of this training were discarded. The buzzer did not sound for any *S* during this period.

Conditioning to buzzer. Following this training, *S*s were randomly divided into six groups, ten animals in each. Groups were conditioned in pairs under different schedules of buzzer presentation. For control groups A and B the buzzer sounded each time a bar-pressing response was made. For groups C and D the buzzer sounded on responses 2, 4, 5, 9, 10, 11, 14, 16, 17, and 20. These groups were the experimental groups. For control groups E and F the buzzer did not sound for any bar response. During this period each *S* was required to press the bar 20 times for 20 pellets of food on each of eight days.

Extinction. Beginning on the day following the last day of buzzer conditioning, three daily extinction sessions of 10 min. each took place. The buzzer sounded on each occasion a response was made by *S*s in groups A, C, and E; the buzzer did not sound for *S*s in groups B, D, and F.

RESULTS

The total responses given in extinction by each group are presented in Table 1. The Bartlett test for homogeneity of variance as described by Edwards (3) was applied to the data, and the obtained chi-square value of 2.70 indicated that the samples were not heterogeneous in variance.

TABLE 1

Total Extinction Scores of Groups Conditioned under Three Schedules of Buzzer Presentation and Extinguished under Two Schedules of Buzzer Presentation

Group	Frequency of Buzzer in Conditioning (in %)	Frequency of Buzzer in Extinction (in %)	Number of Extinction Responses
A	100	100	755
B	100	0	574
C	50	100	719
D	50	0	727
E	0	100	402
F	0	0	637

TABLE 2

t-Values of the Differences in Number of Extinction Responses

Group	B	C	D	E	F
A	2.82** A	.56 A	.45 A	5.50** A	1.84 A
B		2.26* C	2.38* D	2.68* B	.98 F
C			.12 D	4.94** C	1.28 C
D				5.06** D	1.40 D
E					3.66** F

Note:—The direction of the difference is indicated by the letter which appears with each *t*.
* Significant at the .05 level.
** Significant at the .01 level.

An over-all analysis of variance applied to the data yielded an *F* ratio of 8.52, a value significant beyond the .001 level. A complete analysis of variance indicated that the main effect of buzzer during conditioning gave an *F* ratio of 10.63. This is significant beyond the .001 level. The main effect of buzzer during extinction gave an *F* ratio of less than 1. The *F* ratio for interaction was 10.51, a value significant beyond the .001 level.

The statistical evaluation of the results in terms of the *t* test is given in Table 2. The error term used in computing the *t* values was obtained by pooling the sums of squares for all six groups (7, p. 245). Degrees of freedom for evaluating each *t* were 54.

The time required for each *S* to produce 20 reinforced responses on each day of conditioning was obtained. The mean for *S*s in groups A and B was 13.04 min., for groups C and D it was 12.68 min., and for groups E and F it was 12.80 min. No significant differences were present.

During conditioning (and extinction) some *S*s were observed pressing the bar lightly, i.e., the force exerted was insufficient to activate the electrical system of the apparatus. These "responses" did not meet the criterion imposed, and they were neither reinforced nor scored. Thus no data are available by which to evaluate the presence of differential patterns of response engaged in by the various groups.

Some evidence regarding "completeness" of extinction is provided by the finding that the mean number of responses given by *S*s during the initial 5 min. of extinction was 16.62, while the mean number of responses during the final 5 min. of extinction was 6.22. Only one *S* failed to offer at least one response during the final 5 min. of extinction.

DISCUSSION

The extinction scores of the experimental groups (C and D) bear most directly on the problem under investigation, and they are the crucial data about which the discussion must center.

The finding that group C gave significantly more extinction responses than groups B and E appears to confirm the position that an intermittently presented neutral stimulus can acquire reward value. The action of the buzzer during extinction for group C apparently was a reinforcing one.

The results also revealed, however, that group D was similarly superior in extinction responses to groups B and E. Since the buzzer was never present in extinction for group D, the superiority of that group over groups B and E clearly cannot be attributed to the secondary reinforcing action of the buzzer. Therefore, whether the superiority of group C over groups B and E can be ascribed to secondary reinforcement is questionable.

It is believed that the results of the experiment can best be explained by employing the principle of stimulus generalization. This explanation is analogous to that given to explain the greater resistance to extinction found after training under conditions of partial primary reinforcement than under conditions of continuous primary reinforcement (12). In the present experiment the presence (or absence) of the buzzer during conditioning and extinction was assumed to be an important component of the stimulus complexes of each. Its presence (or absence) during the two situations was one means by which the amount of similarity between each could be varied. The principle would permit the prediction that groups for which stimulus complexes in extinction were more similar to those prevailing during conditioning would yield greater resistance to extinction than groups for which stimulus complexes in extinction were less similar. In terms of the presence of the buzzer from conditioning to extinction, groups A and F operated in conditions of greatest similarity, B and E in conditions of least similarity. Groups C and D fall somewhere between these two extremes.

The superiority of groups C and D over groups B and E could be explained in terms of stimulus generalization in the following manner. During the conditioning period for groups C and D, the buzzer was a part of the stimulus complex on half the occasions a response was made, while absence of the buzzer was a part of the stimulus complex on the other half. An extinction situation comprised of either buzzer or no-buzzer thus reproduced a part of the stimulus complex present in conditioning. The change in stimulus complex for groups B and E from conditioning to extinction, however, was of a greater magnitude. Group B proceeded from 100 per cent buzzer to no-buzzer, while group E proceeded from no-buzzer to 100 per cent buzzer. Thus the extinction situations for groups C and D were objectively more similar to conditioning than were the extinction situations for groups B and E. This difference could account for the greater resistance to extinction exhibited by groups C and D. In addition, the number of extinction responses given by groups C and D was approximately the same, a finding consistent with a stimulus generalization hypothesis.

Other findings may be explained by stimulus generalization, e.g., the superiority of A over B and E, and F over E. Stimulus generalization cannot account, of course, for the failure of F to exceed C and D.

The viewpoint that the findings of this experiment may be interpreted in terms of stimulus generalization has important ramifications in that it casts doubt upon the interpretation of other experiments in which resistance to extinction has been attributed to the action of secondary reinforcement. Extinction performance may have been prolonged, not because of any acquired reward value of certain stimuli, but because the presence of those stimuli afforded a greater objective similarity between conditioning and extinction than was the case when those stimuli were not present. Bugelski's experiment (2), for example, is susceptible to this dual interpretation.

Other experiments, especially those in which stimuli closely associated with reward in one situation are able to produce learning in another situation (4, 9), are probably best interpreted as demonstrations of secondary reinforcement.

The present experiment failed to demonstrate clearly the differential effects of secondary reinforcement independently of the effects of stimulus generalization. It is suggested, therefore, that resistance to extinction is not a satisfactory method by which to demonstrate the presence of secondary reinforcement unless the factor of generalization is held constant.

Because the extinction record of group C is subject to a dual interpretation, it is believed that an interpretation of the performance of that group as demonstrating secondary reinforcement is not appropriate. It is concluded, therefore, that the experiment provided no unequivocal evidence that an intermittently presented neutral stimulus can become a secondary reinforcer.

It is suggested that a better method for detecting the action of secondary reinforcement is one in which a neutral stimulus closely associated with reinforcement in one situation is shown to be able to produce learning in another, unrelated situation. This method overcomes the ambiguity of interpretation involving secondary reinforcement and stimulus generalization.

SUMMARY

This experiment was performed to determine whether an intermittently presented neutral stimulus could become a secondary reinforcing agent.

Six groups of 10 rats each were conditioned to press a bar for food. For one pair of groups a buzzer sounded on half the occasions the bar was pressed. For a second pair of groups a buzzer sounded each time the bar was pressed. For the final pair of groups the buzzer did not sound at all during conditioning. In extinction, the buzzer sounded when one group in each pair pressed the bar. The buzzer did not sound when the other group in each pair pressed the bar.

It was found that the intermittent presentation of the neutral stimulus during conditioning led to a significantly greater number of extinction responses, regardless of whether the stimulus was present or absent in extinction (groups C and D), than did the schedule of presentation of the stimulus for the two groups in which the stimulus was present repeatedly in conditioning and absent in extinction (group B), and absent in conditioning and present repeatedly in extinction (group E). No unequivocal evidence was provided, therefore, that an intermittently presented neutral stimulus could acquire reward value.

An attempt was made to point out the role played by stimulus generalization in studies involving secondary reinforcement, and a suggestion was offered relative to a more satisfactory demonstration of secondary reinforcement.

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Received August 21, 1953.

INCIDENTAL LEARNING UNDER CONDITIONS OF UNREWARDED IRRELEVANT MOTIVATION

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The problem of incidental learning of cues for which an animal is not motivated originally arose as an approach to the latent-learning controversy between the reinforcement and cognition learning theorists. Recently the emphasis has shifted from a controversy of the theoretical interpretation to an experimental search for the factors pertinent to incidental learning. The "typical" incidental learning experiment consists of a training series during which the animal is not motivated for the cue-to-be-learned and a test series during which the animal is motivated for that cue. Incidental learning is said to occur if performance on the test series is facilitated by the training with the cue. The problem is that of exploring the conditions of training which alter performance during the test series.

With respect to motivation during the training series, two main types of incidental learning experiments have been reported. In the first type the animals were satiated during training in a single-unit T or Y maze (4, 5, 6). Food or water was placed in one of the end boxes. During the test series when the animals were deprived of either food or water, they showed a marked ability to choose the appropriate side. In the second type the animals were trained under a drive which was different from that used during the test series, i.e., during training they were irrelevantly motivated. Three arrangements of reward have been used during the training period.

1. It seems well established that with an asymmetrical arrangement of rewards an animal trained while highly motivated for one goal object will show no evidence of incidental learning on test runs with changed motivational state (6, 7, 9).

2. The condition of symmetry of reward has also yielded no evidence of incidental learning (2, 3).

3. On the other hand, it appears that rats irrelevantly motivated, but receiving no reward during training, show incidental learning when relevantly motivated during the test period. Strange (8) reports that rats which were thirsty and climbed over food to get out of one end box during training showed a pronounced food-going tendency as compared with the control group when tested after being deprived of food. The control group received no training prior to the test series. Under the conditions of training described it seems possible that an explanation other than incidental learning could account for this difference, at least in part. The control group received the same deprivation and free exploration in the empty U maze but did not receive a training series of 48 trials in the maze as did the experimental group. The greater sophistication of the experimental group with the maze could conceivably account for much of the difference in the performance of the two groups. A finding of Walker (10) appears to support Strange's results but is also inconclusive.

We consider it of importance to determine whether it is the occurrence of the irrelevant drive per se or the rewarding of the drive during training which accounts for the inability of other investigators to demonstrate incidental learning under conditions of an irrelevant drive. Since the experiments of Strange and Walker do not provide an unequivocal answer, it is desirable to repeat Strange's study using more adequate control.

METHOD

Subjects

Twenty female hooded and 20 male albino rats between six and eight months old at the beginning of the experiment were divided equally into experimental and control groups. All animals were reared in the Florida State University laboratory.

Apparatus

A simple T maze was used. Guillotine-type doors operated by a string and pulley arrangement and located at the start box, choice point, and end boxes controlled the movement of the animal through the maze. The top of the maze was wire mesh, and it was possible to view the animals in the maze through a mirror. The entire maze was painted gray.

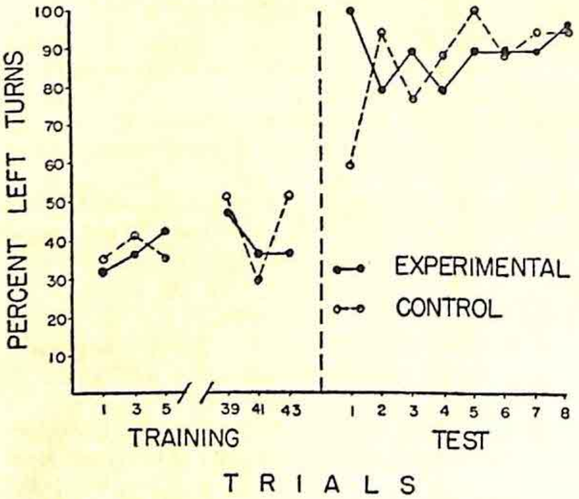

FIG. 1. Percentage of turns toward the end box containing food during the training and test series

Procedure

Habituation series. The animals were handled each day for 14 days prior to the start of the habituation series. On the first day of habituation water deprivation was started and each animal explored the empty T maze for a 5-min. period. On the following three days each *S* received three trials per day in the empty maze. For every trial the animals were detained 15 sec. in the end box before removal. The results of these nine free trials were checked for evidence of position preference. No animal went to the same side for more than six of the nine trials.

Training series. After habituation the training series began. The 23-hr. water-deprivation schedule was continued throughout this period for both groups of animals. During the 11 days of training each animal was given four trials per day. On the first and third trials the animals were allowed a free choice. On the alternate trials they were forced to the wing of the T opposite that chosen on the preceding trial. The animals were detained 15 sec. in the end box before removal to the transporting cage. The choice of left or right was recorded for each trial. During the training period food was placed in the left end box for the experimental animals only. The food used as the incidental cue-to-be-learned was in the form customarily used in the maintenance of the animals, biscuits of Purina Laboratory Chow. The amount of food was such that the forefeet of the animal rested on the pellets when it had fully entered the goal box. No water was given to either group in the maze. When the animals were returned to the home cages they were given water for 1 hr.

Test series. Following the last trial of the training series food was removed from the cages and 23 hr. later the hungry, nonthirsty animals began the test series. Food was placed in the left end box for both the experimental and control groups. Each animal was given four free trials per day for two days. When the correct turn was made, *S* was allowed to eat for 30 sec. When the wrong choice was made, *S* was detained in the end box for 15 sec. before removal.

RESULTS

One animal from the experimental group and one from the control group were eliminated because a position habit developed during training. The criterion of a position habit was seven consecutive free choices to one side out of the last ten training trials. Two animals of the control group were eliminated because they refused to run. They made no progress in the maze during a 15-min. period for two consecutive days.

Figure 1 shows the results of the training and test trials. Our analysis centers upon the first test trial when the animals were relevantly motivated for the first time. Of the 17 control animals, 10 scored a successful turn left to food, whereas all 19 experimental animals were successful. Using Fisher's exact method (1) for calculating the probability of the difference between the frequency of choices of the experimental and control groups on the first test trial, a p of .002 was obtained. The difference between the performances of the two groups on the first trial of the test series is highly significant.

DISCUSSION

This research has not attempted to test the cognition or reinforcement theories of learning. It is a study of a condition favorable to the phenomenon of incidental learning, which, we believe, is in need of experimental clarification first and theoretical explanation next. In this experiment the handling of the experimental and control animals was identical except for the presence of food in the left end box during the training of the experimental group. The animals of this group seemed no more interested in the food in the end box than in any other aspect of the maze. None of them was seen to nibble on the food.

The results of this study are in general agreement with those of Strange (8) that incidental learning occurs under conditions of an unrewarded high irrelevant drive during the training series. A quantitative difference is to be noted. For 16 trials of the test series the performance of Strange's control animals was inferior to that of the experimental animals. In our study the control animals equalled the performance of the experimental animals on the second test trial. This difference is apparently a function of the habituation of the control animals to the maze. Strange did not give the thirsty control animals training trials in the maze although both groups had a period of free exploration prior to being placed on the deprivation schedule. In our study both groups received equal handling and an equal number of training trials.

The experiments (2, 3, 6, 7, 9) in which the irrelevant drive was rewarded either symmetrically or asymmetrically failed to demonstrate incidental learning. It appears, then, that it is the reward of the irrelevant drive, or the lack of it, rather than the irrelevant drive itself which determines whether incidental learning will occur during the training.

SUMMARY

Two groups of rats were given 44 training trials in a single-unit T maze under a thirst drive which was not rewarded by maze activity. Food was placed in one end box during the training of the experimental group. Following training all the animals were deprived of food for 23 hr. All 19 of the experimental animals made a successful first turn toward the food while only 10 of the 17 control animals made a successful turn on the first trial. The difference in performance was highly significant. The experiment demonstrates that incidental learning may occur under conditions of an unrewarded irrelevant drive.

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Received February 1, 1954.

A TECHNIQUE FOR OBTAINING RAPID DRIVE DISCRIMINATION IN THE RAT

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Most contemporary learning theories demand that organisms be able to discriminate their drive states. In fact, for any theory which takes an evolutionary approach, e.g., Hull's, this point is quite crucial if the theory is to account for animals' learning to "satisfy" the needs necessary for survival.

Physiologically great differences can be found between the internal effects of hunger and those of thirst. Hence one might expect that it would be easy to demonstrate drive discrimination. Paradoxically, it has been very difficult to do so—much more difficult than to demonstrate discrimination of external stimuli, e.g., horizontal or vertical striations (1, 2, 3).

The possibility occurred to us that the discrimination of external stimuli has been easier to demonstrate than the discrimination of internal ones because of the differences in the experimental methods employed. There are three obvious differences between the two kinds of experimental procedures usually applied to the two problems, and for each of these differences we propose a resolution.

First, in a discrimination problem involving external stimuli, the onset of the stimulus occurs when the animal reaches the choice point. In the typical drive discrimination problem the stimuli which arise from hunger (or thirst) commence and gradually grow in intensity in some nonmaze setting such as the home cage. Therefore, a maze was constructed in which the animals would live at the choice point, so that the onset of the drive stimuli occurred only at the choice point.

Second, in external stimulus discrimination problems the animal usually is not removed from the goal box in the presence of the discriminandum (discrimination stimulus). However, in drive discrimination experiments, the animal is typically given only a few seconds for consummatory behavior, and consequently when the animal is removed from the goal box, the discriminandum (hunger or thirst) is acting at almost full strength. Our procedure allowed 30 min. to 1 hr. for feeding or drinking in the goal box—sufficient time to satiate the animal.

Finally, in most external stimulus discrimination problems the stimuli are well defined. On the other hand, in a drive discrimination problem the crucial stimuli usually do not act independently but are confounded by other stimulus complexes. That is, if the typical deprivation schedule is used, an animal that is "hungry" is also suffering a water deficit owing to a decrease in total intake, and conversely, a "thirsty" animal is suffering a food deficit. While this fact has been acknowledged quite often, it has been relegated to footnote status. In a drive discrimination problem, however, it is imperative that the internal stimuli arising from hunger and thirst be as "pure" as possible. In order to obtain "purer" drive states, we instituted a maintenance schedule described in a recent experiment by Verplanck and Hayes (4). Their results suggest that in order to obtain a "pure" hunger drive an animal should be given only dry food for 23 hr. and then only water for 1 hr. At the end of this hour, the animal was "maximally" hungry as measured by consummatory activity, and apparently not thirsty. Similarly the procedure for making an animal thirsty was water followed by dry food.

METHOD

Subjects

Twelve naive male rats, approximately 100 days old, from the University of California colony were used.

Apparatus

The inside dimensions of each maze unit are shown in Figure 1. The mazes were made of ½-in. plywood painted gray except for the farthest parts of the goal boxes, which were black or white. The goal boxes and alleys had an inside height of 4½ in. and the home cage inside height was 5 in. The entire maze was covered with ½-in. hardware cloth, as was the floor of the home cage. There were guillotine doors at each goal box and at both doorways of the home cage. One home cage

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[1] The authors wish to acknowledge their gratitude to Dr. David Krech for his generous assistance.

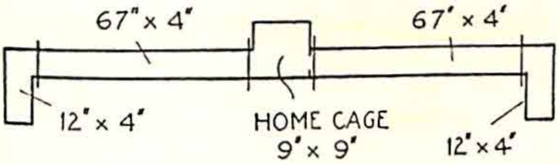

FIG. 1. Top view of maze unit

doorway was 4 in. by 4½ in., the size of the alley, while the other doorway was a 2-in. round hole. These units were stacked three deep with 8 in. between them, in two arrays.

Procedure

Pretraining. The animals were pretrained for two to four days by placing them in the maze with all the doors open, and with no food or water in the home cages. Both food and water were put in both goal boxes. The animals were thus free to explore and to eat and to drink in the goal boxes. Each animal was handled for 5 min. a day during this period. On the last day of pretraining the animals were put in their home cages with both doors closed. Half of them were given food and half were given water.

Learning. Each day during the learning period food was removed from those animals which had had it for 22 hr., and they were given water for 1 hr. Similarly, those that had had water for 22 hr. had their bottles taken away and were given food for 1 hr. This is the aforementioned Verplanck-Hayes method for making the former hungry and the latter thirsty. At the conclusion of the 1-hr. ingestion period all food and water were removed from the home cages. After a period of not less than 5 min., the doors were opened and each animal ran one trial.

When the animal entered the correct goal box, the door was dropped behind it, and the animal was retained for either 30 or 60 min. When it entered the incorrect goal box, it was allowed to leave (the correction method). The door of the incorrect goal box was closed as soon as the animal left, to discourage rampant exploring, i.e., an animal could obtain entrance to the incorrect box only once a day. A trial was not scored as an error unless an animal ran as far as the doorway of the wrong goal box. Thus an animal was not penalized for making a false start in the wrong direction. (This was the scoring method used by Hull [2] and Leeper [3].)

For half the animals, food (dry powder) was in the goal box approached through the round doorway and water was in the goal box approached through the large alley-size doorway. For the other half this arrangement was reversed.

Following the consummatory period the animals were returned to their home cages and their deprivation schedules were reversed. Hence the sequence of correct responses was an alternation series. The possibility of an animal's responding correctly by means of an "alternation hypothesis" was checked by altering the sequence for each animal just prior to attaining criterion. No indication of an alternation hypothesis was revealed.

TABLE 1

Trials and Errors to Criterion for Each Animal

Rank Order	Trials	Errors
1	10	1
2	11	2
3	12	2
4	14	4
5	17	4
6	17	5
7	23	7
8	26	7
9*	—	8+
10*	—	10+

* Discontinued after 20 trials because of no tendency to break position habit.

Two groups of six animals were run and the procedure was changed slightly for each group in order to ascertain if either the length of the pretraining ("exploring") period (two to four days) or the time in the goal box (30 min. or 1 hr.) affected the learning. No differences were found between the groups.

The animals were run to a criterion of nine correct runs on ten consecutive days.

RESULTS

Two animals of the original 12 were discarded. One was discarded because it refused to enter either goal box after a door was inadvertently dropped on it, and the other because it refused to leave the home cage within a period of 2 hr. for the five days we attempted to run it.

Learning proceeded at a spectacular rate. The number of trials and the number of errors made prior to attaining criterion for the ten animals run are tabulated in Table 1. A median of 17 trials was required to reach the criterion. A median of 4.5 errors was made prior to attaining criterion. The learning curve remained above 80 per cent after seven days. Leeper's curve is approximately the same at seven days, but his procedure allowed five trials a day. In Hull's experiment 180 days (five trials a day) were required to achieve 80 per cent.

These results are all the more remarkable in that, owing to the pretraining used, not only were the animals learning the position of food and water, but they probably also had to do some unlearning. In the pretraining food and water were in both goal boxes and therefore, we would have every reason to suppose that an animal would have an expectancy that both goal objects would be located in both goal boxes—and this expectancy would have to be extinguished by the differential reward in the learning trials.

SUMMARY AND CONCLUSIONS

Contemporary learning theories demand that an animal be readily able to discriminate its drive states. But, paradoxically, drive discrimination has been difficult to demonstrate heretofore.

We have resolved the paradox by demonstrating rapid drive discrimination. The rate of drive discrimination obtained in the present experiment compares favorably with the simplest of "sensory" discriminations, thereby providing empirical support to the proposition that drives or biological needs are readily discriminable.

It is suggested that the success of the present experiment is due to the fact that our experimental design incorporated the usual features found in external discrimination problems. The pertinent aspects of this design were: (*a*) onset and termination of the discriminanda occurred in the learning apparatus, and (*b*) a Verplanck-Hayes deprivation schedule was employed, thus "purifying" the relevant "internal stimuli."

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Received February 22, 1954.

A FURTHER STUDY OF SECONDARY REINFORCEMENT AND THE DISCRIMINATION HYPOTHESIS

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A recent report from this laboratory (1) was concerned with the relation between the concept of secondary reinforcement (3) and the discrimination hypothesis—the assumption that resistance to extinction increases with the similarity between conditions of training and extinction (4, 6). Specifically, the question was asked whether the decrease in resistance to extinction which follows a change in the afferent consequences of response can be fully explained in terms of the elimination (or the distortion by neural "interaction") of stimuli previously associated with primary reinforcement. To answer this question, an experimental situation was devised in which the transition from training to extinction was more readily discriminable in the presence of a secondarily reinforcing stimulus than in its absence—a situation in which the effects of discriminability and of secondary reinforcement were opposed.

Under conditions of random partial reinforcement, rats learned to traverse a runway and enter a goal box. On half the trials they were rewarded in a box of one color (e.g., white), while on the remaining trials they found a box of the opposite color (e.g., black), in which there was no reward.[1] Then the animals were divided into two matched groups, one extinguished with the white box (group II-S) and one extinguished with the black (group II-N). In which group should extinction have been more rapid? The principle of secondary reinforcement suggests that response should have been better sustained by the white box, the one previously associated with primary reinforcement; if the effects of change in the afferent consequences of response are to be fully accounted for in terms of this principle, extinction must have been more rapid in the animals run to black. For the animals run to black, however, the early extinction trials represented no discriminable departure from the training series (of which nonreinforcement in the black box was an integral part), while for the animals run to white the consequences of the very first extinction trial (nonreinforcement in the white box) represented a set of conditions never before encountered. On the assumption that *any* discriminable change in afferent consequences—irrespective of previous relation to reinforcement—tends to impair the stability of response, extinction should have been more rapid in the animals run to white. This assumption was supported by the results obtained, and the prediction derived from the principle of secondary reinforcement was contradicted.

The present paper reports a repetition of the experiment described. The repetition differed from the original principally in that the distribution of practice was considerably increased. It was designed to test the generality of the earlier results and to explore the remote possibility—considered in the original report (1, pp. 461–463)—that they were influenced by traces of the afferent consequences of response which might have been carried over from trial to trial.

METHOD

Subjects

Twenty-six experimentally naive rats, bred in the laboratory, were studied. They ranged in age from three to four months at the beginning of the experiment.

Apparatus

The apparatus employed may be described as a combination elevated runway and single-window jumping stand. The runway was 3.75 in. wide and 7.66 ft. long. At its distal end was a goal box containing a 6-in. by 6-in. window. The animal entered the box by jumping a 9-in. gap from the end of the runway to an unfastened card in the window. The purpose of this arrangement was to prevent the animal from seeing the interior of the goal box until the terminal response had been made. The entrance to the goal box was set in a funnel-like surround which served to eliminate abortive behavior and to channel the terminal jump. The entire apparatus was painted mid-gray except the card in the

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[1] For expository convenience we deal only with the animals that were rewarded in the white box and nonrewarded in the black, although the two colors were balanced in the design of the experiment.

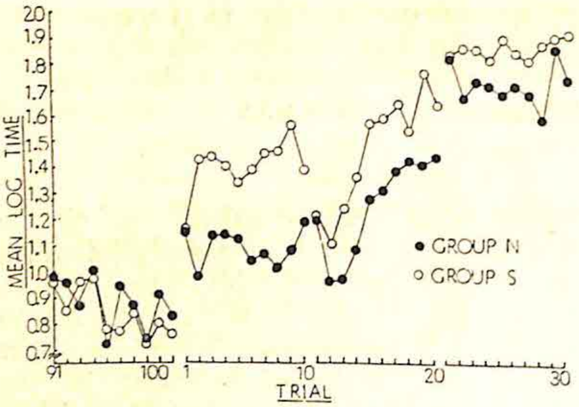

FIG. 1. Performance of the two groups on the last day of training and on the first three days of extinction.

window of the goal box (which was covered with ½-in. vertical black-and-white stripes) and the *interior* of the goal box (which, at different times, was either mid-gray, black, or white). The experiment was conducted in the homogeneous Dome Room of the rat laboratory.

Procedure

Preliminary training. The animals were placed on a 24-hr. feeding schedule designed to reduce them gradually to 80 per cent of their satiated body weight. By varying the amount fed after each day's trials on the basis of weight loss in the preceding 24-hr. interval, each animal could be brought very close to the 80 per cent level at the start of the next day's trials. The animals were fed for brief periods in the gray goal box and then taught to enter it by jumping a gradually increasing distance (to a maximum of 9 in.) from the end of the runway, first to the open window and then to the striped card. Each jump was rewarded with a few seconds of feeding from a cup of wet mash in the gray goal box.

Experimental training. Each animal was given ten trials per day for a period of ten days. A trial consisted of a run from the beginning of the runway to its end and a jump from there to the striped card in the window of the goal box. The animal remained in the goal box for 20 sec. and was then transferred to an individual mesh waiting cage for the intertrial interval, which was never less than 15 min. and often longer. (The animals were run in squads, with the intertrial interval for each animal being determined by the time required to give one trial to each of the others in its squad.) On each trial the time which elapsed between placing the animal on the runway and its jump to the goal box was measured with a stop watch. If on any training trial the animal did not reach the goal box in 90 sec., it was manually guided in the direction of the goal and encouraged to jump from the end of the runway. All animals were reinforced (20 sec. of feeding with wet mash) on five of the ten daily trials. Reinforcement and nonreinforcement were scheduled in accordance with selected Gellermann orders (2).

On each training trial the interior of the goal box was either white or black, and for each animal one of the colors consistently accompanied reinforcement while the other consistently accompanied nonreinforcement. Of the 26 animals, 14 were reinforced in white and nonreinforced in black; the remaining 12 animals were reinforced in black and nonreinforced in white. To ensure the complete absence of food in the goal box on nonreinforced trials, separate boxes were used for reinforced and nonreinforced trials. The procedure thus necessitated the construction of four interchangeable goal boxes—two with white interiors and two with black interiors.

Extinction. At the conclusion of the training series, the animals were paired for reinforced goal-box color and performance during training, a process which resulted in two matched groups of 13 rats each; the extinction series was then begun. Ten nonreinforced trials per day were given. As on nonreinforced training trials, the animals were confined in the empty goal box for 20 sec. after entry and then transferred to the mesh waiting cages. The intertrial interval was controlled as it had been in training, and again the minimum interval was set at 15 min. Runs were timed as before. If an animal did not reach the goal box in 90 sec. on any given trial, it was removed from the runway and placed in its waiting cage until its next scheduled trial. The criterion of extinction was two successive incomplete runs of this kind, and work with each animal was discontinued after it met this criterion.

The two matched groups of animals were treated in exactly the same manner, with one exception. Each animal in group S (the secondary reinforcement group) was extinguished with the goal-box color which had been associated with reinforcement during the training series, and each animal in group N (the reversal group) was extinguished with the goal-box color associated during training with nonreinforcement. Thus, those animals of group S which had been rewarded in white and nonrewarded in black were extinguished with white, while those which had been rewarded in black and nonrewarded in white were extinguished with black. In the case of group N, on the other hand, animals rewarded in white and nonrewarded in black were extinguished with black, and those rewarded in black and nonrewarded in white were extinguished with white.

RESULTS AND DISCUSSION

The performance of each of the two groups on the last day of training and on the first three days of extinction is plotted in Figure 1 in terms of mean log time per trial. In training, of course, the performance of the two groups was very much the same, since they were selected by pairing animals on the basis of their behavior during that part of the experiment. In extinction, however, the two groups differed markedly, with group S (the secondary reinforcement group) showing much less resistance. The curves of Figure 1 closely resemble those obtained in the previous experiment with massed practice (cf. 1, Figure 2, p. 460), except that extinction was somewhat more rapid in the present experiment than in the earlier one. One very interesting feature of the curves for both reversal groups (the present group N and the previous group II-N) is the consistent fall in running time from the first to the second extinction trial in each daily series. That the effect cannot be attributed merely to some sort of warm-up process is suggested by the fact that a quite opposed effect seems to operate in the secondary reinforcement groups (the present group S and the previous group II-S). It almost seems as if the response tendency is temporarily strengthened by an encounter with the goal box previously associated with nonreinforcement.

The results of the experiment as a whole certainly support the conclusion that the response tendency under scrutiny weakens less rapidly when the animal is run to the goal box previously associated with nonreinforcement. The extinction series was terminated after seven days, by which time all the animals of group S had reached the criterion of two successive incomplete responses. For the entire seven-day period, the mean log time per trial was greater in group S than in group N. The mean difference was 0.188, significant beyond the .01 level of confidence (t for paired replicates = 3.08, with 12 *df*). When the same results were obtained under conditions of massed practice in the previous experiment, the possibility was considered that they might be explained, at least in part, by the carry-over of the afferent consequences of response from trial to trial. Group II-N may be said to have been reinforced on about 25 per cent of the training trials for response to a stimulus compound which included traces of the experience of nonreinforcement in the box used for extinction, while group II-S did not (during training) experience nonreinforcement in the box which it subsequently encountered in extinction and consequently was never reinforced for responding in the presence of the aftereffects of that experience. This rather forced interpretation cannot apply in the present case because the interval between training trials was never less than 15 min.

The results at hand do not, of course, make it possible to discard the principle of secondary reinforcement. Experiments such as that of Saltzman (5), for example, clearly demonstrate that, as a consequence of association with primary reinforcement, previously neutral stimuli may come to play a selective role in behavior. The present results suggest only that the principle is insufficient in itself to account for the effects upon extinction of change in the afferent consequences of response, and that in the situation here employed it is overridden by some other set of determinants. In training under conditions of partial reinforcement, the animal apparently learns about the occurrence of nonreinforcement per se and about stimuli associated with it. This learning influences the animal's perception of the transition from training to extinction and hence (by the discrimination hypothesis) the stability of response. How the animal can learn about nonreinforcement presents a rather difficult problem for drive-reduction theory. Perhaps its solution will only be found in a systematic account of perceptual learning.

SUMMARY

Rats were trained to traverse a runway and enter a goal box (black or white) under conditions of random 50 per cent reinforcement and distributed practice. During training the animals were consistently reinforced in a goal box of one color and nonreinforced in a goal box of the opposite color. During extinction, group S (the secondary reinforcement group) was run to a goal box of the color previously associated with reinforcement, while group N (the reversal group) was run to the color previously associated with nonreinforcement. The results obtained were closely similar to those of an earlier experiment of the same general design in which practice was massed: group S extinguished significantly more rapidly than did group N. It is concluded that the principle of secondary reinforcement is inadequate to deal with the effects on extinction of change in the afferent consequences of response. The results of the experiment may be understood on the assumption (*a*) that any discriminable change in the afferent consequences of response tends to facilitate

extinction, and (*b*) that the discrimination of change may be based upon learning about *non*reinforcement and about stimuli associated with it.

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Received January 27, 1954.

RELATIONAL DISCRIMINATION OF INTERMEDIATE SIZE IN THE CHIMPANZEE[1]

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If, after learning to choose the *largest* or the *smallest* stimulus in a set of three, an animal transposes the solution up or down the size continuum, no perception of relations need be assumed; once the proper gradients of generalization have been selected, the results can be explained—as Spence has shown—in terms of excitatory and inhibitory effects derived from the reinforcement and nonreinforcement of afferent components (4, 5). If, on the other hand, an animal has learned to choose the *intermediate* member of the set, the mere occurrence of transposition constitutes conclusive evidence against the component theory, which requires that the animal continue to choose the previously reinforced stimulus (6). In neither case, however, does the failure of transposition necessarily invalidate the concept of relational perception; the fact that an animal responds to certain absolute features of a stimulus object presented in some arbitrary context does not justify the conclusion that it is incapable of response to relations.

Some years ago, Spence looked for evidence of transposition in the behavior of six adult chimpanzees after training them to discriminate the intermediate member of a set of three squares differing quite markedly in size (6). Each of the animals responded predominantly to the previously reinforced stimulus, although there was some evidence for the development of "a different basis of response than an absolute one" (p. 270) in the course of "reversal training" (a sequence of problems in which the roles of common elements shifted with the context in which they appeared). Spence concluded that his component theory was confirmed by the data of his experiment, suspending judgment on the consequences of reversal training until further investigations could be made. Recently Spence has extended his theory to permit differential response to *aggregations* of stimuli—visual-spatial compounds and conjunctions of visual elements ("transverse patterns")—in situations which do not involve the differential reinforcement of afferent components (1, 7). According to the new version of the theory, the outcome of reversal training can be explained as an instance of transverse patterning (a conditional rather than a relational phenomenon); however, transposition must continue to be denied when the training problem is one which can *in principle* be mastered in component terms.

The possibility of spontaneous relational organization in the solution by chimpanzees of the intermediate-size problem (as distinct from the no longer crucial effects of reversal training) was further investigated in the present experiment, which differed from that of Spence in two important respects: (*a*) The difference in size among the stimuli to be discriminated—the difference *within* sets—was considerably less; the ratio of areas within critical sets was 1:1.32 as compared with the ratio of 1:1.60 employed by Spence. (*b*) A new method of testing for relational perception was devised in order to minimize the difference *between* the sets of stimuli used in training and testing.

The first modification was introduced on the assumption (derived from human experience) that spontaneous relational organization is most likely to appear when differences among the stimuli to be discriminated are small. In an experiment with the rat, Saldanha and Bitterman (3) found evidence which supports this assumption; while quite discrete stimuli, such as horizontal and vertical stripes, were discriminated as readily in isolation as in conjunction, opportunity for comparison was necessary for discrimination between more similar stimuli. From this point of view, negative results in an investigation of the possibility of relational perception at any given phylogenetic level—e.g., Spence's study of intermediate size with the chimpanzee (6) or Grice's work on mode of stimulus presentation with the rat (2)—are inconclusive when the limits of discriminability have not been explored. (In the present experiment, plans were made for further reduction of within-sets differences if reliable evidence of transposition should fail to appear.) The second procedural modification (designed to minimize between-sets differences) was adopted on the following assumptions: (*a*) that the animal may learn something about the absolute magnitudes represented in a set of stimuli, even a highly homogeneous set which can be differentiated only on a relational basis; and (*b*) that the initial functional equivalence of training and testing sets depends upon the similarity in absolute properties.[2] It is well to note, however, that according to Spence's viewpoint neither of these procedural modifications should increase the likelihood of transposition following training on an intermediate-size problem which is capable of solution in component terms.

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[1] The experimental work was done in the Radiobiological Laboratory of the University of Texas and the United States Air Force.

METHOD

Subjects

Four adult chimpanzees, two mature females (No. 2 and No. 3) and two somewhat younger males (No. 1 and No. 4), were studied. All had previous discriminative experience, but in problems which were functionally unrelated to that of the present experiment.

Apparatus

A string-pulling apparatus was employed which could be wheeled up to the home cages of the animals. The stimuli designed for the work were nine cubical wooden boxes, each of which was open at the top and painted black both inside and out. The boxes were designated in order of size with the numbers *1* to *9*. Each face of the smallest box was 9.00 sq. in. in area, and the corresponding value for each successive box in the series increased by a factor of 1.15. On each trial three of the boxes were presented (8 in. apart) at a distance of 30 in. from the cage. Each box was mounted on a narrow track and equipped with a uniform string by means of which it could be pulled to the cage by the animal. Any given box could be baited with a small piece of preferred food which served as reinforcement. The baiting was done behind an opaque screen which was lowered between trials and raised at the beginning of each trial. The apparatus was so designed that the animal could determine whether a given box was baited only by pulling it all the way to the cage and reaching inside.

Procedure

Each animal was trained first to a criterion of 16 out of 18 correct responses on problem I—boxes *1*, *5* (positive), and *9* (ratio of areas 1:1.75). There were 18 trials per day by the correction method; if on any trial the first choice was incorrect, the animal was permitted to make a second and, if necessary, a third choice, with each trial being terminated by a reinforced response. The spatial arrangement of the three boxes was systematically varied. After each animal reached the criterion, it was trained in the same manner and to the same criterion on problem II—boxes *3*, *5* (positive), and *7* (ratio of areas 1:1.32).

In the second stage of the experiment the animals were tested with each of two new sets of stimuli—*2*, *4*, *6* and *4*, *6*, *8*. The ratio of areas in each set was the same as in problem II (1:1.32), but the difference between each new stimulus and the corresponding stimulus of problem II was considerably less (1:1.15). There were four daily series of 18 trials each. Of these, 12 were differentially reinforced trials with boxes *3*, *5* (positive), and *7* (problem II); systematically interspersed among them were six testing trials—three with *2*, *4*, *6*, and three with *4*, *6*, *8*—in which *any* choice was rewarded. In the four days of testing, each testing set was presented 12 times, twice in each of the six possible spatial arrangements.

RESULTS AND DISCUSSION

Under ideal circumstances—if there were no pre-experimental size preferences, and if the two stimuli of the pairs *4-6*, *3-7*, and *1-9* were in fact functionally equidistant on the size continuum from the previously reinforced point *5*—the hypothetical gradients of excitation and inhibition established in training would be symmetrical about point *5*, and Spence's theory would require that the animals choose boxes *4* and *6* equally often in the trials with each of the two testing sets. Under any circumstances, however, the theory predicts that the choices of the animals should be restricted to boxes *4* and *6*, and that the frequency with which either box is chosen should not, after component training, depend on "the nature of the total stimulus pattern" (7), i.e., on whether the third stimulus presented is *2* or *8*. In the 24 tests, therefore, the number of intermediate choices (the number of choices of *4* in the set *2*, *4*, *6* plus

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[2] Interestingly enough, where an animal is trained simply to choose the larger or smaller member of a pair of stimuli (or the largest or smallest member of a set of three), Spence's nonrelational theory quite clearly permits the deduction, which has been regarded as one of the most striking demonstrations of its power, that the probability of transposition varies inversely as the absolute difference between training and testing sets (5). A comparable effect in the discrimination of intermediate size (if it were demonstrated) could not, however, be explained in the same way, because in the case of intermediate size Spence's theory permits no transposition at all.

TABLE 1

Days to Criterion in the Training Problems and the Distribution of Responses in 24 Tests

Animal	Days to Criterion	Choices on Test Trials				Number of Intermediate Choices
		2	*4*	*6*	*8*	
1	10	1	11	0	—	
		—	5	7	0	18
2	14	0	11	1	—	
		—	4	8	0	19
3	16	0	10	2	—	
		—	6	6	0	16
4	12	0	6	6	—	
		—	3	9	0	15

TABLE 2

Distribution of the Responses of Animal No. 1 in Four Days of Reversal Training (18 Trials per Day)

Day	Choices				Number of Intermediate Choices
	2	*4*	*6*	*8*	
1	0	8	1	—	
	—	5	4	0	12
2	0	7	2	—	
	—	4	5	0	12
3	0	8	1	—	
	—	1	8	0	16
4	0	9	0	—	
	—	1	8	0	17

the number of choices of *6* in the set *4, 6, 8*) should not, on the average, exceed 12. A reliably greater number would indicate the operation of a relational process.

The principal results of the experiment are presented in Table 1, which shows the number of days required by each animal to reach the final criterion in the training problems and the distribution of responses to each of the two sets of stimuli presented in the subsequent tests. Performance on the testing trials clearly suggests the interplay of two distinct tendencies, an absolute preference for one of the two critical stimuli (*4* or *6*) and a relational preference for intermediate size. Animals No. 1, No. 2, and No. 3 show an absolute preference for box *4* which coincides with the relational preference in tests with *2, 4, 6*—hence the greater frequency of intermediate responses to that set—and which opposes the relational preference in tests with *4, 6, 8*; in animal No. 4, on the other hand, the absolute preference is for *6* rather than *4*. The reality of the relational preference is indicated by the fact that in the 24 tests every animal made a number of intermediate choices greater than 12, the value expected in terms of component theory; the mean number of intermediate choices for the group (17.0) was significantly greater than 12 beyond the .02 level of confidence ($t = 5.5$ with 3 *df*). Further evidence is available on the reliability of the relational tendency in animals No. 3 and No. 4, the two that made the lowest numbers of intermediate choices in the first four days of testing. In a fifth day of testing by the same procedure, No. 3 made five and No. 4 made six intermediate choices in the six trials (three with *2, 4, 6* and three with *4, 6, 8*).

After the transposition tests, animal No. 1 was given four days of differentially reinforced reversal training with sets *2, 4, 6* and *4, 6, 8*, which were presented in random sequence and in all possible spatial arrangements; as in the original training, there were 18 trials per day by the correction method. From Table 2 it may be seen that the number of intermediate choices made by the animal was above the chance level on the first day and rapidly approached the maximum on subsequent days. This performance clearly demonstrates "a different basis of response than an absolute one"—to use Spence's elliptical formulation—but it probably does not represent the qualitative break with the effects of the original learning which Spence's theory requires. The behavior of the animal on the first day of reversal training revealed (as did its behavior in the previous transposition tests) the simultaneous operation of two distinct preferences—absolute (for the smaller of the two critical stimuli) and relational (for the intermediate stimulus irrespective of absolute properties)—with the former rapidly disappearing in the face of differential reinforcement. The reversal problem did not elicit a new level of functioning. It merely resolved a conflict between two response tendencies—relevant but incompatible—which were in evidence at the conclusion of the original training.

SUMMARY AND CONCLUSIONS

Four adult chimpanzees were trained to discriminate the intermediate member of a set of three stimuli which differed in size. In subsequent tests the animals displayed a significant tendency to transpose the solution, although evidence of absolute preferences also appeared. Then one of the animals—beginning at a level of accuracy greater than chance—rapidly learned a reversal problem involving two sets of stimuli in which positive and negative values of common members shifted from set to set. The results of this experiment will not yield to analysis in terms of components or aggregations of components. They point unmistakably to the operation of a relational process in the discrimination of intermediate size by the chimpanzee.

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Received December 21, 1953.

DISCRIMINATION LEARNING IN THE CANARY

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The oddity problem has been solved by the monkey, chimpanzee (cf. 1), and rat (7). Can the canary learn to respond to the odd stimulus of a set of otherwise identical stimuli? If the answer is in the affirmative, can the canary learn to respond to the odd stimulus when stimulus values are reversed from trial to trial?

METHOD

Subjects

Three canaries (labeled A, B, and C) participated in the experiments after overnight food deprivation. Birds A and B had previous experience on a string-pulling problem, and Bird A learned to position a truck or box beneath a suspended food bin to retrieve food otherwise inaccessible (3).

Apparatus

An apparatus quite similar to that used by Harlow (1) in his experiments on discrimination learning with primates was adapted to the canary. A food tray was placed outside the cage at a height where it was necessary for the canary to jump from its customary perch within the cage to a perch placed directly in front of the tray. In the preliminary experiments there were three food wells; in the main experiments there were nine food wells.

PROCEDURE AND RESULTS

The canaries readily learned to jump to the perch in front of the food tray and push aside an object which hid a pellet of grain in the well below. In the prolonged series of preliminary experiments (three stimulus objects) Birds A and B failed to learn to select the odd stimulus consistently. Although the learning of the two birds was quite efficient, even when stimulus reversal was involved, the attempt was made to facilitate learning by substituting 9 stimulus objects instead of the previous 3. Nissen and McCulloch (2) had shown that the chimpanzee more readily learned to select the odd stimulus when it was set against 11, rather than only 2, identical stimuli.

Since the selection of the odd stimulus was apparently facilitated when set against eight identical objects, we proceeded to the main question. If the stimulus values are reversed from one trial to the next, will the birds consistently select the odd stimulus? The stimulus objects—a small black chess pawn and an aspirin tablet—were selected from the objects used in the preliminary experiments. In all experiments the canary was permitted to correct its errors. The results were striking—Birds A and B each had 13 hits in 18 trials. (The probability of getting a hit on the basis of chance alone is 1/9.) This experiment was repeated four times for each bird with 20 trials to each experiment. Of the total of 98 trials for each bird, Bird A had 76 hits and Bird B, 83. The results are even more significant when it is realized that the birds, after having displaced only one of the incorrect stimulus objects, went to the correct object. Such trials, however, were counted as errors.

Bird C (a naive bird) was introduced to the trial-to-trial discrimination reversal problem after ten reinforcements in pushing aside a coin which hid food. The stimulus objects again were the black chess pawn and the aspirin tablet (eight of one kind and one of the other). This bird solved the problem after 360 trials. In the final block of 20 trials (beginning with trial 361) the bird attained the criterion of at least 15 hits.

Control experiments showed that the birds were neither responding to an alternation tendency nor to olfactory cues.

DISCUSSION

The obtained results seem to be in contradiction to Spence's theory of discrimination learning. According to Spence, "the excitatory tendency of the positive stimulus . . . is increased in strength in a cumulative manner with each reinforcement while that of the negative stimulus . . . is weakened cumulatively with each failure of reinforcement" (5, p. 77). Moreover, in his theory "there is no assumption of a perception of the relational character of the situation" (4, p. 435). Spence's theory seems to imply that learning cannot take place in a situation in which there is reversal of stimulus values from trial to trial; such stimulus reversal would prevent the consistent strengthening of either an excitatory or inhibitory tendency in relation to a given stimulus. However, the three birds learned to select the odd, rewarded stimulus; Bird C mastered the problem despite trial-to-trial reversal from the very outset of training. These results are consistent with a perceptual interpretation: the birds learned to respond to the odd stimulus of a set of otherwise identical stimuli. Such an interpretation makes it unnecessary to assume, as Wodinsky and Bitterman suggest in a similar experiment, that lower organisms are capable of an "abstract level of functioning" (6, p. 141).

SUMMARY

Three canaries were trained in a discrimination problem which can be subsumed as a special case of the oddity problem. All canaries were able to select the odd stimulus even when reversal of stimulus values was involved. These results were interpreted as being consistent with a perceptual interpretation.

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Received January 15, 1954.

THE EFFECT OF SPATIAL CONTIGUITY ON DISCRIMINATION LEARNING BY RHESUS MONKEYS[1]

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Aristotle's original formulation (7) of the principle of association by contiguity placed stress upon both temporal and spatial contiguity. This duality of emphasis remained throughout the history of Associationism, receiving specific formulation, for example, in James Mill's (10) discussion of synchronous order and successive order.

In recent years, however, temporal contiguity has remained as an important theoretical construct and experimental variable, whereas spatial contiguity has been relatively neglected. Because of the importance of spatial contiguity and the paucity of pertinent studies, additional systematic exploration of this variable is desirable.

The present study was designed to investigate the relationship between acquisition in a discrimination situation and various degrees of spatial discontiguity between the stimulus objects and the locus of response, with temporal factors held relatively constant.

METHOD

Subjects

Four adult rhesus monkeys, numbers 137, 147, 150, and 159, were *S*s in this experiment. Approximately four years earlier, these animals had been thoroughly tamed and adapted to the general test situation, and since that time had participated in a large number of discrimination, discrimination-reversal, and delayed-response problems at the University of Wisconsin Primate Laboratory.

Apparatus

The apparatus consisted essentially of a vertical test panel designed to fit the standard test tray carriage of the Wisconsin General Test Apparatus, which has been previously described and illustrated (8).

The test panel, shown in Figure 1, was a gray-painted wooden board 26 in. sq. and 1 in. thick with two vertical slots each 2 in. wide extending from the bottom of the panel to the top. The base of the test panel was 24 in. by 9½ in. and contained two food wells centered at the bottom of the slots and 15 in. apart from center to center. The vertical slots were so constructed that 2-in.-sq. wooden blocks could be inserted flush with the surface of the test panel. The response blocks rested on the base of the apparatus and could be moved backward, exposing the food wells. The stimulus blocks, which could be moved vertically in the slots up to 12 in. above the response blocks, were held at specified heights by means of pins inserted into holes drilled in the margin of the slot at the back of the panel. One stimulus block was painted white and the other black. The white stimulus block was the positive stimulus for all animals.

Two gray doors which closed behind the slots prevented the animal from seeing *E* and, in addition, provided a relatively homogeneous gray field. The only interruptions in the surface of the test panel were the vertical slots.

Procedure

The test procedure was as follows: The pins were inserted at a predetermined level at the beginning of each series of four trials. On each trial, the stimulus blocks were lowered simultaneously into the slots in positions determined by Gellermann sequences (6). Both response blocks were withdrawn, the correct food well was baited with a raisin, the blocks were replaced simultaneously, and the doors were simultaneously closed to prevent possible differential sound cues. The forward opaque screen of the Wisconsin General Test Apparatus was raised, and the test tray carriage was pushed toward the animal and stopped at a position previously determined to lie between 50 and 90 per cent of the animal's maximum reach (3). Following the animal's choice the carriage was withdrawn, the forward screen lowered, and the next trial begun. The noncorrection technique was used throughout. All the described manipulations were carried out on every trial so that sound cues would be constant whether or not the locus of the positive stimulus had changed from that of the previous trial.

Experimental Design

Spatial discontiguity was measured in terms of the distance separating the upper margin of the response block and the lower margin of the stimulus block. The effect of the four magnitudes of separation, 0, 1, 2, and 4 in., was measured. These magnitudes of separation are subsequently referred to as conditions 0, 1, 2, and 4, respectively.

The monkeys were given 64 test trials a day for 20 days. A daily session consisted of 16 problems of 4 trials each, and the condition of spatial separation remained unchanged during the 4 trials of a given problem. Each condition (0, 1, 2, and 4) was presented four

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[1] This research was supported in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation.

[2] Now at Yale University.

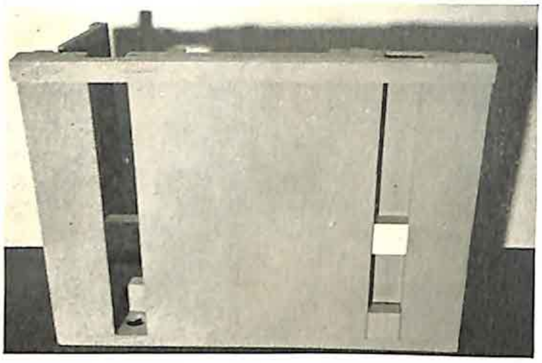

FIG. 1. The test panel

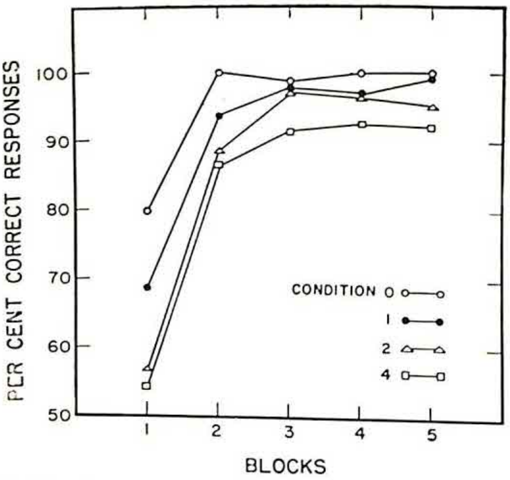

Fig. 2. Percentage of correct responses for blocks of days

times during each day's session, with the sequence of presentation being determined independently for each animal and for each problem by permutation of latin squares taken at random from the Fisher and Yates tables (4). This method provided that no condition occurred for the second time until all other conditions had appeared.

RESULTS

Separate statistical measures for the several aspects of the data were computed because the marked skewness and heterogeneity of variance of the data, which remained even after transformations, precluded meaningful use of an over-all analysis of variance.

Learning

The percentage of correct responses plotted against five blocks of four days each with magnitude of spatial separation as parameter is presented in Figure 2.

The curves for each condition show a marked initial rise and a subsequent apparent approach to an asymptote at a high level of performance. Furthermore, the data of Table 1 show that the learning under each condition and for all conditions combined was significant at the .01 level of confidence. The values of t reported were obtained by computing a difference score (D = percentage of correct responses on block 5 minus percentage of correct responses on block 1) for each animal under each condition, obtaining the mean value of D ($\bar{D}$) for each condition, and dividing by the corresponding standard error.

TABLE 1

Over-all Learning for All Conditions

Condition	D	s_D	t	$p <$
0	.203	.016	12.72	.01
1	.305	.039	7.82	.01
2	.387	.037	10.46	.01
4	.379	.068	5.57	.01
Combined	.318	.029	10.97	.01

TABLE 2

Total Correct Responses for 20 Days

Condition	Animals			
	159	150	147	137
0	307	307	308	303
1	288	292	289	298
2	279	272	272	289
4	275	242	266	285

The null hypothesis tested was that $\bar{D} = 0$. The probability values associated with t indicate that this hypothesis may be rejected for all conditions at the .01 level of confidence. That is, there is a significant improvement in performance from block 1 to block 5.

Effect of Experimental Conditions on Performance

Table 2 presents the total correct responses by all animals for all conditions over the entire 20 days.

Inspection of the data shows that when the conditions are placed in rank order from that under which performance was best to that under which performance was poorest, the order 0, 1, 2, 4 is obtained for each animal. There are no inversions or negative cases. If it is assumed as a null hypothesis that one resulting order is as likely as any other, the probability of obtaining 0, 1, 2, 4 for any one animal is $1/x$ and the probability of 0, 1, 2, 4 for all animals is $(1/x)^4$, where x is the number of possible orders. The value of x will be given by ${}_nP_r = 4!/0! = 24$. Thus, the probability of obtaining the rank order of 0, 1, 2, 4 for all animals is $(1/24)^4$, and hence the effects of conditions on performance are statistically significant.

Corroborating evidence was obtained from an analysis of variance computed on the error scores for the first block of four days, from which it was possible to eliminate heterogeneity of variance by the $\sqrt{X + .5}$ transformation. The F value for the experimental conditions was 20.79, which for 3 and 9 *df* is significant at the .01 level of confidence, supporting the argument presented above.

DISCUSSION

The data of the present experiment indicate that spatial discontiguity between the differential stimuli (CS) and the locus of response adversely affects discrimination learning by monkeys, and that the relationship between the degree of stimulus contiguity and efficiency of performance is orderly.

Although the authors failed to find previous formal studies of the effect of spatial contiguity on efficiency of learning, there are a number of reports in which spatial discontiguity between CS and locus of response was inadvertently introduced through inadequacies of apparatus or other factors.

Andrew and Harlow (1) in a study of concept formation trained their monkey *S*s to discriminate between two differential stimuli which were supported, by means of wires, 2 in. above identical wooden bases. Learning was far slower and many more errors were made than when comparable objects were placed directly over the food wells. Similarly, Gellermann (5) made no progress after 500 trials in training two chimpanzees to discriminate when the stimuli were mounted on the front of two boxes and the animals were required to lift the appropriate box lid to obtain a reward. Gellermann states: "At this point the forms were taken out of the form-presentation frame and placed in positions adjacent to the box lids. Under these conditions, the apes learned to respond correctly in about 50 trials apiece" (5, p. 12). Actually, Gellermann's revised apparatus was so arranged that unnecessary spatial discontiguity between CS and locus of response resulted, and the relatively inefficient performances by Gellermann's chimpanzees may have resulted in part from this factor.

Recently Wodinsky, Varley, and Bitterman (12) have investigated discrimination learning of rats in a four-window jumping apparatus. In one condition the rats jumped to differential stimulus cards placed in the two end windows, and in another condition they jumped to the appropriate window in an end position in response to differential cards placed in the center windows. In all tests the rats were more efficient when they jumped to the stimulus card offering the differential cue than when they jumped to a card lateral to the differential cue card.

Much of the apparatus used by the early comparative psychologists proved to be spectacularly inefficient, doubtless in part a result of spatial discontiguity between CS and locus of response, or between CS and US. The Yerkes-Watson discrimination apparatus (13) is a classical example, for the US was removed from the CS the maximal distance and direction which the size of the apparatus permitted.

Although the effect of spatial contiguity on learning has attracted little attention, it should be noted that there have been investigations of spatial contiguity of CS and locus of response as it affects generalization (2) and of the spatial relationships among unlearned signs and releasers (11). A more detailed discussion of the role of spatial contiguity in standard learning situations is presented by McClearn (9).

Although spatial contiguity has been measured and described simply as a function of stimulus-separation distance, the problem is in all probability much more complex, and such factors as the plane of stimulus separation may play an important role. Furthermore, psychological spatial discontiguity is probably not linear and may be logarithmic.

SUMMARY AND CONCLUSIONS

Four monkeys were trained on a discrimination problem with 0, 1, 2, and 4 in. of vertical

separation between the differential stimuli and the locus of response. Sixty-four trials were given each day for 20 days. An inverse relationship was found between magnitude of spatial separation and efficiency of performance. The relative disparity among conditions of separation decreased with training, all curves approaching asymptotes at levels above 90 per cent correct responses.

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Received December 31, 1953.

"CUE" VS. "REACTIVE INHIBITION" IN PLACE AND RESPONSE LEARNING

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The experiment by Tolman, Ritchie, and Kalish (9) on spatial learning in rats produced data that were used to support the interpretation of "what is learned," suggested by Tolman *et al.*, and implicitly to reject the reinforcement interpretation as stated by Hull (5). This experiment required one group of animals to make alternate responses depending upon the starting point in order to find food at the same place, and another group to make identical responses from alternate starting places to find food at alternate places. Tolman *et al.* discovered that the first group, the "place" group, learned with fewer errors and in fewer trials than did the other, "response," group. The generalized interpretation of these results was that animals that learned to go to a specific place for food learned more efficiently than animals that learned specific responses (if this in fact was what they learned).

An experiment was performed by Blodgett and McCutchan (1) to demonstrate that spatial learning is neither easier nor more "primitive" than response learning, and by Thompson and Thompson (7) to demonstrate that spatial learning was an artifact of the techniques used in training (massed trials).

The Blodgett and McCutchan experiment served to indicate that environmental content was a necessary condition for the existence of spatial learning. Munn (6) suggests that the existence of the environment required the response group to learn an abstracted response. Both these statements support the view that animals can learn places in a well-structured environment, but the limiting effects of the environment have only been touched on by the Blodgett and McCutchan study (1).

On the other hand, the Thompson and Thompson (7) experiment presumably revealed a methodological flaw in the California technique. They pointed out that in the original place-learning study the use of massed trials would operate in favor of the place-learning group because of the effects of "reactive inhibition." This refers to the tendency of an animal to avoid repeating a response identical to the one preceding. If it could be shown that massed trials account for the difference between the two groups, severe limitations would have to be applied to the interpretation of the experiment as support for cognitive theory.

In Hull's system the magnitude of reactive inhibition is a function of work and, unlike habit strength, dissipates as a (monotonic) function of time. Therefore, with massed trials, the order of responses required by the place-learning group would make any reactive inhibition which was generated aid their performance. In testing this hypothesis Thompson and Thompson found, using spaced trials, no significant difference between place and response groups.

But Thompson and Thompson, while correcting the methodological flaw in the original design, came up with one of their own. It seems evident a priori that if place learning is dependent on the establishment of "cognitive maps," the completeness of the map is by definition dependent on the presence of a terrain to be mapped. Thompson and Thompson, in utilizing an undifferentiated black curtain around their maze, effectively eliminated, as far as the visual environment of the experimental animals was concerned, the presence of any place to which that group could respond. ("Presence," as used here, means presence in the perceptual field of the organism; "terrain" refers to that environment which is in a fixed functional relationship to the path over which the organism locomotes.)

The present experiment was designed to reproduce the environmental conditions that Blodgett and McCutchan have shown are necessary for the existence of place learning, and to discover if the interpretation in terms of reactive inhibition is sufficient. Also, to test whether environmental properties are the sufficient condition for the existence of the phenomenon, variations in the experimental environment were introduced.

METHOD

Apparatus

An elevated T maze, identical to the maze used by Tolman, Ritchie, and Kalish, was constructed (9). It was painted flat black and was modified for use with group III by the installation of two flashlight bulbs centered on top of the wire curtain rod in front of the food boxes. These bulbs were painted black on three sides, so that when turned on, a directional light was cast down the long arm of the maze. To the dark-adapted observer, it was extremely difficult to make out any of the surrounding environment. The food boxes at either end contained a pan, filled before each set of trials with a mixture of warm milk and dry puppy biscuit. The maze was located in a room approximately 12 by 30 ft. The ceiling was about 18 ft. high, and during the training of groups I, II, and IV there was sufficient unbalanced illumination and other extramaze environment to insure orientation. The home cages were about 12 ft. from the maze, and groups I, II, and IV were kept in a special cage to the right of f-1 during trials. The rats in group III were kept in a cage immediately under the choice point during their trials.

Animals

Four groups of eight rats each were used. They were mixed male and female albinos of a Wistar strain. At the beginning of training they were approximately two months old and weighed (mean weight) 80 gm. They had been on a dry food maintenance schedule for two weeks before beginning training. The feeding cycle was established as an alternate-day feeding to satiety, followed by a 24-hr. deprivation. During training, groups I (place learners) and II (response learners) were run and fed between 2 and 5 P.M. on Tuesday, Thursday, and Saturday. Group III *S*s (place and response learners) were run between 8 and 10 P.M. on Monday, Wednesday, and Friday. Group IV *S*s were run on Monday, Wednesday, and Friday afternoon. All groups were fed so as to experience 24 hr. of total food deprivation before any block of trials. Water was available in the home cage at all times.

Procedure

All four groups were given the same preliminary training. Section f-1, f-2 was placed about 7 ft. from its final position and at right angles to it. On the first day the rats were fed by hand in each of the two food boxes for 5 min. each. They were then placed in the center of the run and allowed to go to either end, where they were removed and returned to the home cages. One-half hour later they were given their regular feeding.

On the second day, with the run in the same position, each rat was started from the center of the run, and a block was placed behind the curtain at the food box toward which they started. Thus, they were forced to return to the other end of the run for food. After feeding for 5 min. they were rerun in the same way two more times. After this, they were returned to the home cages, and ½ hr. later they were given their regular ration. This training was continued for two more days.

After this the regular training began. The maze was moved to its final position. The training of each group was conducted as follows:

Group I. A trial was given to determine the position preference of the rat. After it had made this choice, it was allowed to feed and then was removed from the situation. The choice made on this trial was recorded, and for every trial thereafter, the rat was forced, by blocking the side originally chosen, to find food at the opposite side. Following the initial trial, each rat was given a block of 6 trials daily, with half the trials starting from s-1 and the other half from s-2. On even days the order was 1-2-2-1-1-2, on odd days 2-1-1-2-2-1. When starting from s-1, the animal found the food at f-1 (or f-2, depending on the original preference); when starting from s-2, *S* found the food at the same point. Therefore, group I was learning always to go to the same food box to find food, while having to make a right or left turn at the choice point, depending upon the end from which it started. Fifteen or 20 min. elapsed between trials for any one rat. This time was used to insure a lessened reactive inhibition. The blocks used were changed every 6 trials, and the run f-1, f-2 was rotated end for end every 6 trials. Records were kept of errors, which were recorded whenever a rat entered upon an improper alley for a distance of 12 in. or re-entered the short arm after crossing the choice point. The criterion for learning was 10 errorless consecutive trials, or 72 trials, whichever occurred first.

Group II. The procedure outlined for group I applies except that the position-preference trial was eliminated. When the trial run started from s-1, the animal was allowed to find food at f-1, with f-2 being blocked. When starting from s-2, the rat found food at f-2 and f-1 was blocked. Thus, the rats had to learn to turn right regardless of the end from which they started. The same interval between trials was used, and the same records were kept. The maze was not rotated for this group, nor were the blocks changed. The criterion was the same.

Group III. Trials were run at night in the dark, the only source of illumination being the small bulbs at one or the other end of the maze. The trials were alternated as with group I, but this group, when starting from s-1, found the open food box at f-1, and the light above f-1 was on. When starting from s-2, the animals found that the food box at f-2 was open and that at f-1 blocked, and the light this time was at f-2. The difference in brightness between f-1 and f-2 was 42 db. This group had to learn always to make a right turn and always to run toward the light. In terms of the definitions proposed by Tolman, Ritchie, and Kalish (9) for the types of learning in groups I and II, group III was developing both a place habit and a response habit. The same records were kept, and the same criterion was used for this group.

Group IV. These animals were run in the same environment as groups I and II. They always started from s–1 and were allowed to find food at f-1. The rats then always had to turn right at the choice point and always started from the same place. The same records and criterion were used.

It is important to emphasize that for groups I and II, the "cues" associated with the response were in each

TABLE 1
Means and Standard Deviations of Number of Trials to Criterion and Errors for All Groups

GROUP	TRIALS		ERRORS	
	Mean	*SD*	Mean	*SD*
I	8.0	8.48	4.6	3.45
II	38.6	22.11	26.9	21.14
III	16.4	13.65	15.2	14.25
IV	1.9	0.64	1.1	0.84

case antagonistic; i.e., the visual cues for group I were consistent with respect to the goal, while the proprioceptive cues instigated by the turning response were systematically varied. For groups III and IV, however, the visual and proprioceptive cues were always invariant with respect to the goal. Group III had limited but invariant visual cues, while group IV had unlimited visual cues which were also consistent with the turning response.

RESULTS

Table 1 shows the means and standard deviations of number of trials required to reach the criterion and number of errors made by each group before reaching the criterion.

The significance of the differences between the groups as measured by the Wilcoxon T test for ranked unpaired replicates gave p values of less than .01 for groups I and II, II and IV, and III and IV. The p for the difference between groups I and IV was less than .05, while the differences between groups I and III and II and III were not significant.

The interpretation of the data presented should take into consideration the fact that two animals in group II (response learners) did not reach the criterion within the 72 trials allowed. Therefore, although a mean error score was computed for group II, the mean value is undoubtedly deflated, since the animals appeared to have developed a "place" habit and were therefore making 50 per cent errors. It should be mentioned that all the rats in group III turned away from the light on the first trial.

DISCUSSION

The Tolman, Ritchie, and Kalish experiment was rerun to allow for the dissipation of reactive inhibition, which had been suggested by Thompson and Thompson as an uncontrolled variable in the original study. Our results, which allowed for control of this variable, were not compatible with those reported by Thompson and Thompson. The only difference in experimental technique between our study and theirs was that the environment for groups I, II, and IV in our experiment provided the animals with more "signs," "cues," or "articulation." If we can assume that the technique of spacing trials minimized reactive inhibition, then we can conclude that control of this variable is irrelevant.

It is suggested by our experiment that the number and consistency of cues are a more effective explanation of the outcome of place-learning experiments than the construct "reactive inhibition." As both Thompson and Thompson, and Blodgett and McCutchan have already pointed out, certain space props in the original Tolman experiment were working against the response group. By the same reasoning, lack of space props must operate against the place group, as has been shown by Blodgett and McCutchan. As Munn suggests, the interpretation on the basis of existing data is difficult. However, our group III may help clarify the situation. This group, although learning the same place *and* the same response, reveals *less* efficiency than the original place group. In this situation there is no possible antagonism of stimulus support, either interoceptive or exteroceptive, for the appropriate response. We would agree with Estes (2) that an interpretation in terms of the sheer number of available cues or signs, i.e., stimulus elements "conditioned to" response categories, perhaps weighted as Hebb (3) suggests for perceptual constancy during locomotion, and which are invariant with respect to the spatial disposition of the "food place," may be both the necessary and sufficient conditions for differences in efficiency of learning. Thus we would suggest that functional significance concerning the eating place accrues to the structure of the organism and the environment during repeated trials. An increase in the "confidence" or "probability" of the response occurs as the number of invariant cues having this functional significance increases.

Using Honzik's (4) empirical data to weight the relative confidences ascribable to cues impinging on various modalities, we can derive the order of rapidity of learning for our four groups. Honzik's data indicate that visual cues are much more important than proprioceptive. Therefore, weighting visual cues heavily in general and considering them equal when their number is small (e.g., group III), we can schematize our outcome as follows:

Efficiency	Invariant Cues	Group
1	VISUAL + proprioceptive	IV
2	$\text{VISUAL} + \dfrac{1}{\text{proprioceptive}}$	I
3	visual + proprioceptive	III
4	$\dfrac{1}{\text{VISUAL}} + \text{proprioceptive}$	II

The use of the reciprocal of the cue indicates that the two modalities are antagonistic. The probability that the outcome for the four groups will be in this order by chance alone is 1 in 24.

We may rightly insist that if response learning demonstrates the simple acquisition of habits with environmental conditions held constant (or, rather, assumed nonexistent), and if S-R theory is designed merely to explain learning under such conditions, then S-R theory lacks the concepts necessary to explain the above data. However, such a negative contribution does nothing to help formulate a cognitive theory. Toward this end it seems wise, in view of the results obtained, for cognitive theoreticians to devote time and energy to an analysis of the perceptual configurations (i.e., Tolman's [8] *S* or differentiation variables) such as "place," "path," "terrain," etc., which seem to be prime factors in determining behavior at the choice point.

Such theoretical formulations are not the goal of the present paper. However, programmatic research directed toward an empirical determination of the effects of variation in stimulus energy and distribution as a function of the experimental route seems fruitful as a first step in the construction of a cognitive theory.

SUMMARY

1. Four groups of rats were run in a T maze with alternate starting places under varying environmental and performance schedules.

2. The rats (group I) that were always run to the same places to find food, regardless of the point from which they started, learned the maze rapidly even though the trials were spaced to allow for the dissipation of reactive inhibition.

3. The rats (group II) that learned always to make a specific turn at the choice point regardless of the starting position, learned most slowly, even with time allowed for the dissipation of reactive inhibition.

4. The rats (group III) that were required to learn with minimum visual environment but had only to learn to make the same turn and go to the same place learned less rapidly than group I but more rapidly than group II.

5. The rats (group IV) that learned to make the same turn to the same place in a perceptually rich environment learned most rapidly.

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Received November 27, 1953.

THE TEMPORAL DISTRIBUTION OF AVOIDANCE RESPONSES

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Several recent studies of avoidance conditioning have utilized a technique in which brief shocks were administered to white rats every few seconds, with no warning signal to indicate an impending shock. Each emission of a lever press by the animal served to delay the occurrence of the shock. Among the data reported were the following observations: If the animal is shocked every time it permits, e.g., 20 sec., to pass without a lever press, it eventually develops a relatively stable rate of lever pressing (8). When the time interval within which it is required to press the lever is changed, the response rate varies also as a function of this interval (9). Furthermore, if two responses are available, each of which delays the shock for a different time interval, it will more often use that response which delays the shock for a longer time (10).

These data suggest that temporal discrimination plays an important role in the avoidance conditioning that results from the above procedure. The strongest indirect evidence against the existence of such a discrimination is provided by the observation that avoidance conditioning occurs when the shock is not terminated by the lever press. In this case it may be asked why time (more accurately, some event occurring regularly in time) should cue lever pressing rather than other behavior, unconditioned or otherwise, which accompanies shock termination. This argument, of course, applies only to acquisition stages of the avoidance response and not to the maintenance stages after it has been well learned.

The present experiment supplies a more direct test of the suggestion that time conditioning can account for some or all of the properties of the avoidance response. Since no exteroceptive warning signal is provided whose onset or termination might delineate the start of an interval, it is necessary to look to the avoidance response itself to perform this function. That is, a time discrimination, if any, must be based upon the occurrence of an avoidance response plus the subsequent passage of time. In this study the frequency distribution of intervals between successive responses served to indicate the presence or absence of temporal discrimination.

METHOD

Subjects and Apparatus

The *S*s were white rats and domestic cats. The general shock and control apparatus has already been described elsewhere (9). In brief, the animals were placed in a small experimental box with a grid floor through which shocks were delivered. A lever protruded through one wall of the box. The cat apparatus was essentially an enlarged version of that used for the rats. A system of relays and timers provided automatic shock control. Total responses and shocks were recorded on electrical impulse counters, with continuous records being taken on Harvard cumulative recorders. A frequency distribution of time intervals between successive responses was automatically tabulated for each session on a combination timing-counting device. A random noise generator masked sounds from the control apparatus.

Procedure

Rats. Brief shocks of fixed duration (0.2–0.3 sec.) occurred every 20 sec. as long as no lever-pressing response was emitted. Any lever press, however, delayed the appearance of the next shock for 20 sec. (R-S interval). In this way a minimum interval of 20 sec. was assured between lever depression and shock. Only the initial depression of the lever delayed the shock; holding the lever down did not affect the interval. Each session lasted 7 hr., and the animals ran every other day.

Cats. The procedure was essentially the same as for the rats except that the animals determined the shock duration. When the shock came on, because of the animal's failure to respond on time, it stayed on until a lever press occurred. In this case the lever-pressing response served both to avoid and escape shock. The period by which each response delayed the shock differed from that used for the rats, being either 21, 30, or 45 sec. The R-S intervals used are identified in the accompanying data. Experimental sessions lasted 2 to 3 hr., and the cats were run daily.

RESULTS

Representative frequency distributions of the time intervals between successive responses are presented for three animals in Figure 1.

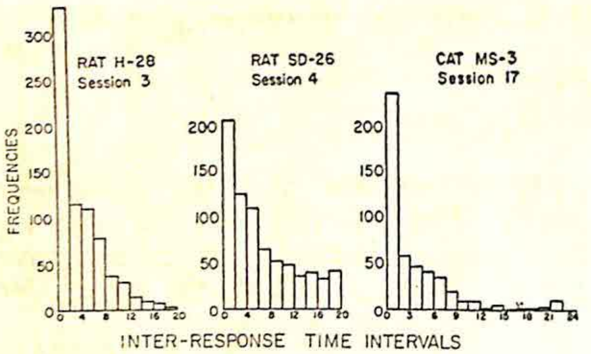

FIG. 1. Frequency distributions of the time intervals between successive responses. R-S intervals are 20 sec. for the rats and 21 sec. for the cat.

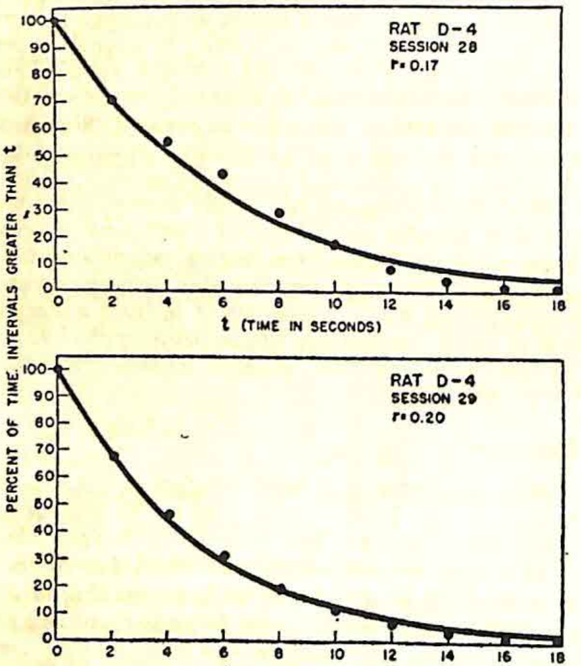

FIG. 2. The percentage of interresponse time intervals greater than *t*, where *t* is time in seconds. Rate of responding in responses per second is *r*. The line through the data is a plot of the equation, $P_{>t} = e^{-rt}$.

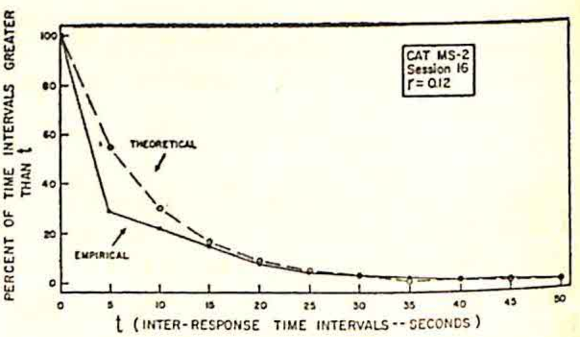

FIG. 3. An example of the Type I deviation from the theoretical assumption of random responding. R-S interval = 45 sec., and *r* is response rate in responses per second.

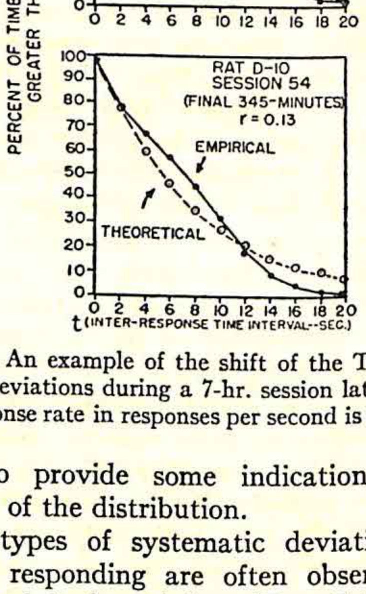

FIG. 4. An example of the shift of the Type I and Type II deviations during a 7-hr. session late in training. Response rate in responses per second is noted by *r*.

Short interresponse intervals predominate, with a general decline in the frequency of longer intervals.

Figure 2 carries the analysis a step further. The equation, $P_{>t} = e^{-rt}$ has been fitted to the cumulative distribution. $P_{>t}$ is the probability of observing an interresponse interval greater than *t*; *r* is the response rate, and *e* is the base of Naperian logarithms. This equation may be derived from the assumption that the responses are randomly distributed in time. Two successive 7-hr. sessions have been included in Figure 2 in order to provide some indication of the stability of the distribution.

Two types of systematic deviation from random responding are often observed. An example of the first of these (Type I deviation) is illustrated in Figure 3. The dip of the empirical function below the theoretical one at short intervals indicates a tendency for responses to occur in short bursts. The Type I deviation is especially prominent at the start of conditioning, but tends to decrease with time, both within and between sessions. Figure 4 (which also contains a Type II deviation) illustrates an extreme example in which the short bursts of responding disappear after the first 75 min. of a session late in training.

The second type of deviation (Type II), often observed in conjunction with the first, is illustrated in Figure 4. The empirical function crosses above the theoretical one, remains higher in the middle range of intervals, and then crosses below it at the longer intervals. This indicates an excessive number of those interresponse intervals which fall between the two points of intersection of the curves.

In addition to its location on the function, this deviation differs from the first in that it tends, with continued training, to become more prominent both within and between sessions. In Figure 4 the increased Type II deviation, along with the decreased Type I deviation after the first hour and a quarter, accompanies a considerable drop in the rate of responding.

DISCUSSION

The data clearly show that time conditioning is not responsible for the avoidance behavior. The shape of the distributions in Figure 1 is the mirror image of what would be expected if a well-developed temporal discrimination were present. Additional emphasis is given to this conclusion by the close resemblance of the cumulative distribution to a function derived from the assumption of random responding in time.

This theoretical assumption, however, is subject to qualifications imposed by two types of deviation from randomness. Of the two, the Type I deviation (short bursts of responses) is the least understood. It is possible to attribute these rapid responses to an emotional effect generated by the shock. The tendency of the Type I deviation to adapt out with continued training gives some support to this suggestion. Experimental procedures designed to identify the controlling variables are presently being tested.

The Type II deviation from random responding is of the sort to be expected if an imperfect time discrimination were to form. In the example of Figure 4 (lower frame), pauses of approximately 2 to 12 sec. between responses occur more often than would be expected on the assumption of random responding, while intervals greater than 12 sec. occur less often than would be expected. The occurrence of an avoidance response appears to initiate a "safe period" during which competing behavior temporarily recovers in strength. In the case of one animal this safe period was observed to increase in duration and effectiveness, with the consequent formation of a rather precise time discrimination (Fig. 5). It must be emphasized, however, that such a discrimination, in either its mild or extreme form, appears only after prolonged exposure of the organism to the experimental procedure, and can in no way be considered necessary for original conditioning of the avoidance response.

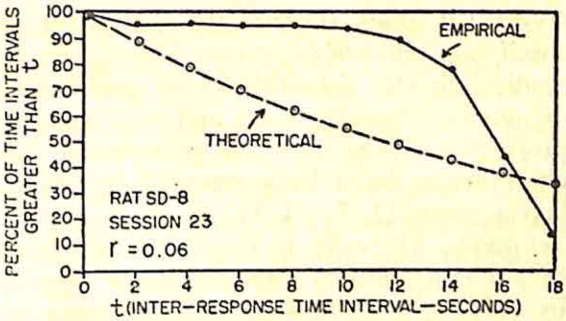

FIG. 5. An extreme Type II deviation indicating a well-developed time discrimination after continued training

General Considerations

The question may be raised as to the relevance of the random or near-random distribution of avoidance responses for current theories of avoidance conditioning. No problem is posed for drive-reduction theories of either the Miller (3) or Mowrer (4) variety. These writers hold that an acquired drive ("fear" or "anxiety") motivates the occurrence of the response, and the termination of this drive reinforces the response. Since the properties of the drive are known from the properties of the behavior observed, it only remains to postulate that, under the present procedure, the acquired drive occurs randomly in time.

A theory which "derives" quantitative properties by postulate is unsatisfactory in many respects. The formulation employed by the writer (9, 10), in line with earlier developments by Hefferline (2) and Schoenfeld (6), also suffers from the defect of being nonquantitative. However, in holding the punishment of nonavoidance behavior to be crucial, it does possess the advantage of specifying observable events which can be studied directly for evidence of randomness, depression by punishment, and other relevant properties. Techniques for performing such observations have been reported by several investigators (1, 7, 10, 11).

Finally, there is a close correspondence between the present data and those reported by Mueller (5). From an experiment on periodic food reinforcement, Mueller obtained frequency distributions of interresponse time intervals which were remarkably similar to those obtained here in an avoidance situation. The resemblance suggests two avenues of future theoretical inquiry: (*a*) an extension to avoidance behavior of Mueller's theory of the relation between measures of conditioning, and (*b*) a search for basic processes common both to avoidance and nonavoidance situations.

SUMMARY

With rats and cats as *S*s, an avoidance conditioning technique was employed in which every lever press delayed a shock for a specified time interval. There was no warning signal to indicate an approaching shock. Frequency distributions were made of time intervals between successive responses.

The frequency distributions indicated clearly that avoidance conditioning in this situation is not a product of time discrimination. Responses were distributed randomly or near randomly in time, with two types of commonly observed deviations from random responding being noted. Theoretical significance of the data was discussed.

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Received January 29, 1954.

MAZE RETENTION DEFICIT FOLLOWING ELECTROCONVULSIVE SHOCK INDEPENDENT OF FEEDING SCHEDULE[1]

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Mirsky and Rosvold (3) demonstrated that rats allowed to feed ad libitum become less hungry following a course of electroconvulsive shocks (ECS), whereas rats kept on an 85 per cent of weight feeding schedule become more hungry. On the basis of these results, it was suggested that the maze deficit in ECS studies using a feeding regime that allows animals to maintain weight was due, at least in part, to the decreased hunger of the shocked rats. It was also suggested that studies in which restricted-weight feeding was employed might not show deficit because of the increased hunger of the shocked rats. The relevant ECS literature appeared to furnish evidence supporting this formulation. Comparing the results of several studies, however, is not completely satisfactory because there are invariably a number of differences between studies in addition to the difference in feeding schedules.

The purpose of the present investigation is to compare two groups of shocked rats on the retention of a food-rewarded maze habit, keeping similar all conditions except feeding schedule. It is predicted that the animals kept on a restricted-weight schedule should perform better following shock than animals fed on a schedule permitting them to maintain weight.

METHOD

Subjects

Thirty-three 150-day-old male albino rats of the Sprague-Dawley strain were housed individually and allowed to feed ad libitum for ten days. They were then placed randomly into one of two groups. The group designated *two-hour* ($N = 16$) was thenceforth permitted to feed for 2 hr. daily on a mixture of two parts water to one part ground Purina Laboratory Chow. The group designated *85 per cent of weight* ($N = 17$), after being starved for one day to determine an empty weight for each animal, was fed on a mash of similar proportions, the amount given daily being adjusted to keep each animal at 85 per cent of its empty weight. Thirty days were allowed to accustom the animals to the 2-hr. schedule or to bring them down to 85 per cent of weight. The rats were weighed before their daily maze trials and fed after the last animal had finished its trials.

Procedure

Maze learning. Following adaptation to the feeding schedule, all rats were given 15 days of preliminary training on the practice problems of the Hebb-Williams closed-field test (1). They were then given eight trials on each of the 12 test problems of this maze, one problem per day. The procedure and problems were identical with those used by Rabinovitch and Rosvold (4) except that both time and error scores were recorded. These measures are termed *learning scores*. Each feeding group was then separated randomly into two groups, a shock and a control group. The two-hour shock group originally contained ten animals, but four died after shock. Thus, there were six two-hour shock *S*s, ten two-hour controls, eight 85 per cent of weight shock *S*s, and nine 85 per cent of weight controls.

Shock. Beginning on the day following the twelfth problem, the rats in the shock groups were given one shock per day for ten consecutive days; the control rats had the alligator clips attached to the ears on each day, but no shock was delivered. The shocking apparatus was that used by Mirsky and Rosvold (3), and it invariably produced a convulsion of the type described as tonic-clonic.

Maze retention. After the ten days of shock or pseudo shock, the animals were again given eight trials on each of the 12 test problems. The time and error measures obtained are termed *retention scores*.

RESULTS

Table 1 presents the mean weights of the various groups at the beginning of the experiment and before the shocks were administered. The weight of a group of nine untreated animals fed ad libitum is included for comparison. It is evident that although the 85 per cent of weight animals are approximately 50 gm. lighter than the two-hour animals before shock, the animals fed ad libitum outweigh the two-hour animals by about 130 gm.

The mean learning and retention scores for both time and errors are summarized in Table 2. The Mann-Whitney U test was used to evaluate differences. Each shock group

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[1] This investigation was supported by the Veterans Administration (Contract VA1001-M3222), with the advice of the Committee on Veterans Medical Problems of the National Research Council, and by the National Science Foundation.

TABLE 1

Mean Body Weight of Experimental Groups at Various Intervals

Time of Measurement	Group				
	Ad Lib. (N = 9)	85-S (N = 8)	85-C (N = 9)	2 Hr.-S (N = 6)	2 Hr.-C (N = 10)
Beginning of experiment	347.6	340.7	339.9	342.6	340.3
Before shock	451.9	268.0	271.9	319.2	324.0

TABLE 2

Total Learning and Retention Time and Error Scores

Measure	Group							
	85-Shock		85-Control		2 Hr.-Shock		2 Hr.-Control	
	Learn.	Reten.	Learn.	Reten.	Learn.	Reten.	Learn.	Reten.
Errors	115.9	168.5	108.8	60.3	121.3	253.0	112.8	83.6
Time (seconds)	894	4362	632	370	1380	7332	1452	722

performed significantly worse than its control group if retention scores or savings scores (learning minus retention) are compared ($p < .001$ for both time and errors, retention or savings). Since learning differences exist between the two shock groups and the two control groups with respect to time scores ($p < .001$ in each case), the time-score retention comparisons employ a difference between difference (learning minus retention) score. Because there was no significant difference in learning error scores between the two shock groups and the two control groups, retention error scores have been compared directly. These comparisons reveal that whereas there are significant differences in retention in the predicted direction between the shock groups with regard to errors ($p = .041$), the difference between the retention error scores of the two control groups is even more significant ($p < .01$). The difference between the retention time scores (corrected for learning differences) of the two shock groups is not significant ($p = .38$).

DISCUSSION

The results indicate that animals kept on a restricted weight schedule did not perform better following shock than animals fed on a schedule permitting them to maintain weight. The retention time scores of the two groups did not differ; the difference in error scores was less than that existing between the two control groups. This would suggest that the variable hunger (depending on body weight) following ECS noted by Mirsky and Rosvold (3) probably does not contribute significantly to the variation among ECS studies in the report of maze deficit following ECS. These studies and the present one used various ways of restricting food intake. In view of the fact that before shock the two-hour groups (although maintaining a steady gain in weight) were 130 gm. lighter than animals fed ad libitum, it might have been more meaningful in terms of the Mirsky-Rosvold (3) effect to have run ad libitum animals in the maze. However, no previous study of the effect of ECS on food-motivated maze running employed such a feeding schedule. Although the present study does not contradict the variations in hunger reported by Mirsky and Rosvold (3), it does indicate that, contrary to their suggestion, the hunger variations consequent upon variations in body weight employed in most of the previous ECS studies probably do not account for the variations in the reports of studies of maze-retention deficit following ECS.

SUMMARY

1. Two groups of rats, one restricted to 85 per cent of weight, the other allowed to feed sufficiently (2 hr. daily) to maintain a steady gain in weight were trained on the problems of the Hebb-Williams closed-field test.

2. Approximately half of each group were given a series of ten electroconvulsive shocks; all animals were then tested for retention of the problems.

3. Both groups of shocked animals performed significantly ($p < .001$) worse than their controls; no difference was discernible between the two differently fed groups in the amount of deficit following shock.

4. It was suggested that the variation among previous studies in food-motivated maze-retention deficit following convulsive

shock is not attributable to variations in the body weight (and consequently, hunger drive) of the shocked animals.

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Received January 20, 1954.

STIMULATION DEAFNESS: A STUDY OF HEARING LOSSES RESULTING FROM EXPOSURE TO NOISE OR TO BLAST IMPULSES[1]

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Since the experiments of Wittmaack (12) and Yoshii (13), the exposure of ears of experimental animals to intense sound stimuli has been a method repeatedly used in the study of hearing because it provides a way to produce lesions of the inner ear elements without damaging the conduction mechanism or the bony shell of the cochlea. A summary of studies done before 1935 has been given by Kemp (2), and discussions of later experiments may be found in the writings of Stevens and Davis (9) and Wever (10).

In addition to the many experiments in which animals have been used as *S*s, numerous studies have been made of the hearing losses incurred by human *S*s exposed to excessive sound levels. Kryter (3) has given a concise, critical review of the latter investigations. Rüedi and Furrer have discussed in some detail the clinical aspects of acoustic trauma (6).

With only a few exceptions, these studies of man and of lower animals have attempted to correlate (*a*) the characteristics of the sound stimulus with inner ear damage as found upon histological examination or (*b*) the characteristics of the stimulus with functional loss as measured by cochlear microphonics or reflex responses of animals or by the audiograms of human *S*s.

In recent studies Smith and Wever (7, 8, 11) and Lurie, Davis, and Hawkins (4) have reported the results of both cochlear microphonic tests and of histological examination of ears exposed to pure tones at high intensity levels.

To complete the picture there is a need for comparable studies in which behavioral tests of hearing are made and intracochlear damage is assessed post mortem. To fulfill this need, a series of experiments was planned. In the first experiment, reported here, temporary hearing losses produced by exposure to noise and permanent losses produced by the blasts of a starting pistol have been studied. Cochleas of the animals suffering permanent hearing loss have been examined and the locus and extent of damage correlated with the hearing losses.

METHOD

The *S*s of the experiment were adult cats. In order to confine hearing tests and noise stimulation to a single ear, one ear of each cat was destroyed surgically.

After recovery from the operation, animals were trained by the conditioned avoidance method to respond to tonal signals by running forward in a rotating cage. Stimulus limens were then determined for frequencies at octave steps from 62.5 to 16,000 c.p.s. For further details of the training and testing procedure, see Neff (5).

After audiograms had been obtained, animals were exposed to intense noise produced by a gas-tube noise generator, the output of which was amplified and fed to a Jensen HNP-51 speaker. The frequency spectrum of the noise, measured from a point within the rotating cage, is shown in Figure 1. A calibrated 640 AA condenser microphone and an RA 1095 preamplifier were used. The output of the preamplifier was measured by a Hewlitt-Packard Model 300 A Harmonic Analyzer with half-band width control set to 145 c.p.s. At this selectivity, the response of the analyzer is attenuated approximately 40 db at 145 c.p.s. on each side of the center frequency. The over-all level of the noise was 107 db re 10^{-16} watts/cm^2. This measure was obtained with the condenser microphone feeding into a Ballantine voltmeter. During noise exposure the animal was unanesthetized and free to move about within the limits of the rotating cage used for conditioning tests. Exposure times of 15, 30, and 60 min. were used. Each animal was exposed for each of these durations; no new exposure was made until there was complete recovery from any hearing loss produced by an earlier exposure. The order of exposure with respect to duration was varied for different animals, i.e., some animals were first exposed for 15 sec., some for 60, and some for 30. Threshold tests were started within 5 min. after cessation of a given exposure and were repeated at intervals until complete recovery from temporary hearing losses occurred.

In a second part of the experiment, anesthetized animals were exposed to the blasts of noise produced by the firing of a .32 caliber starting pistol. Again hearing tests were made at intervals until complete recovery had occurred or until a deficit remained at the same level over a period of several weeks. If hearing returned to normal, additional exposures to the blast stimulation were given until a permanent loss had been produced. The animals were then killed, the cochleas were prepared for histological examination, and graphic plots were made of the inner ear damage.

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[1] This study was supported by the Office of Naval Research, under Contact N6 ori-20, Task Order XXIV, ONR Project NR 140 608.

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RESULTS

Temporary Deafness

Eight animals were exposed to noise according to the procedure described above. In every case postexposure tests revealed a temporary hearing loss which was greatest for frequencies in the range from 2000 to 8000 c.p.s.

For the exposure times (15, 30, and 60 min.) used in the present experiment, no regular relationship was found between amount of hearing loss and length of exposure time. For some animals there was an increase in hearing deficit with increase in exposure time; for others the reverse was true, the greatest loss occurring after the 15-min. exposure period. And for a third group the losses were almost identical for all three exposure times.

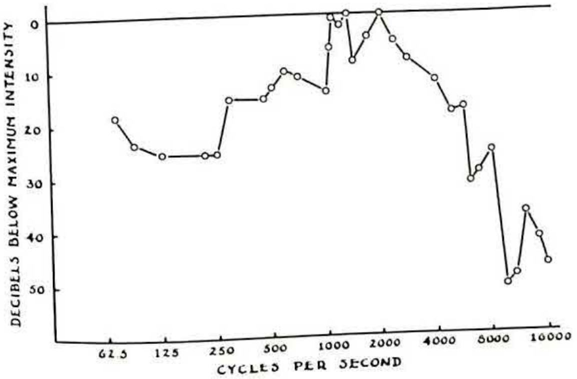

FIG. 1. Frequency spectrum of noise used to produce temporary deafness. See text for method of measurement.

The hearing losses produced by the noise were temporary in every case. Tests were repeated after each exposure until the threshold curve had returned to normal. The curves in Figure 2 show the gradual recovery of function which typically occurs. The time intervals between postexposure tests were not the same for all animals, so exact comparisons of rate of recovery cannot be made. Although individual differences were again great, in general, length of time for recovery was more closely related to amount of immediate postexposure deficit than to length of exposure time.

In three animals (cats 1, 2, and 3), nearly complete recovery from the hearing losses produced by initial exposures to the blasts of the .32-caliber starting pistol was found. Although the immediate losses were no greater than those produced by noise stimulation in the same animals, recovery was much slower and small losses at the frequencies maximally affected were still present when the animals were again exposed to the gun blasts. For cat 1 this was 6 days after first exposure; for cat 2, 16 days; and for cat 3, 27 days. In these three animals the initial, fairly widespread effect produced in the inner ear by the gun blasts was almost but not entirely reversible.

Permanent Deafness

Irreversible losses in hearing were produced in seven cats by exposure to the blasts of the .32-caliber starting pistol. In most cases immediate postexposure loss was greatest for frequencies in the 2000 to 4000 c.p.s. range.

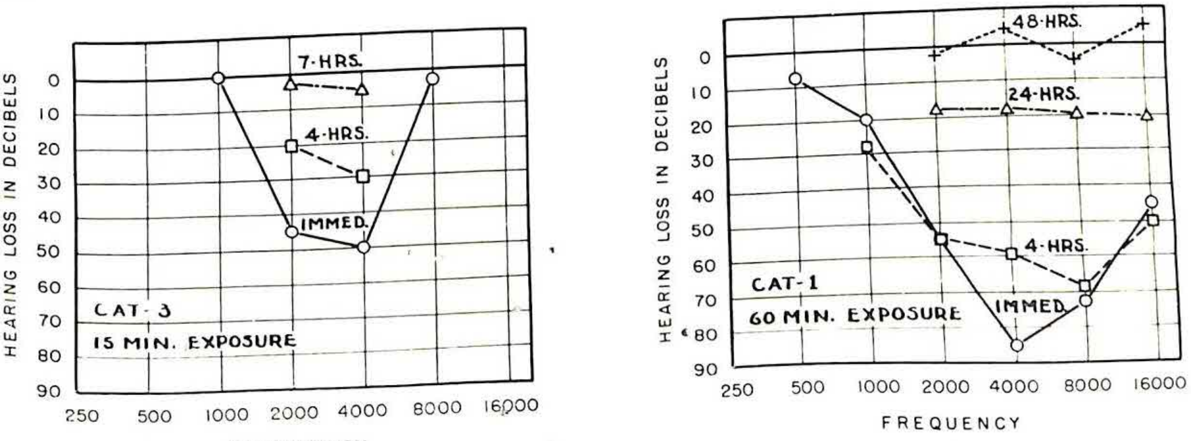

FIG. 2. Audiograms taken at different intervals after exposure to noise

However, one animal, cat 10, had greatest impairment of hearing for the frequencies below 2000 c.p.s., which suggests damage to the middle ear conduction mechanism, and cat 7 had almost complete loss of hearing for all frequencies.

For all animals except cat 3, partial recovery of function occurred during the weeks following exposure. Thresholds usually reached a stable level by the end of four weeks. Cat 3, which was subjected to repeated exposures before a permanent loss was produced, had almost complete loss of hearing when first tested 2 days after the final exposure. When tested again, 8 days after exposure, it responded to all frequencies, but only at high intensity levels. This partial recovery was temporary; by 18 days after exposure the loss was greater again throughout the frequency range. During the period from 18 to 74 days the audiogram remained at a nearly constant level. No responses could be obtained for frequencies of 2000 c.p.s. and above at the highest intensities which could be produced (see Fig. 3).

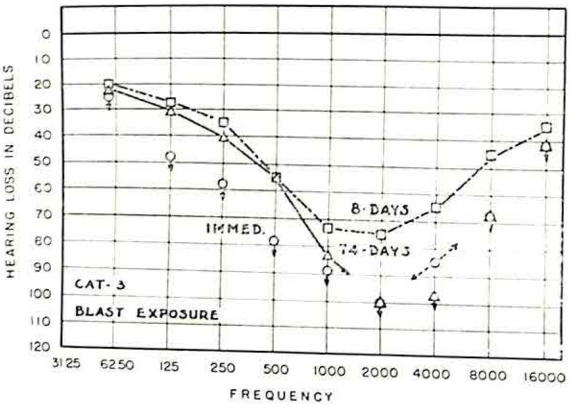

FIG. 3. Severe, permanent loss of hearing produced by blast stimulation

Histology

Hair cells, ganglion cells, and the nerve fibers from spiral ganglion to hair cells appeared normal in all parts of the cochleas of cats 1, 2, 6, 9, and 10. The external sulcus cells were torn or disrupted in the upper basal and lower middle turns of the cochleas of cats 2 and 10 (Fig. 4); the cells of Claudius and Boettcher were also damaged but over a much narrower range. This damage to the external supporting cells may be simply an artifact

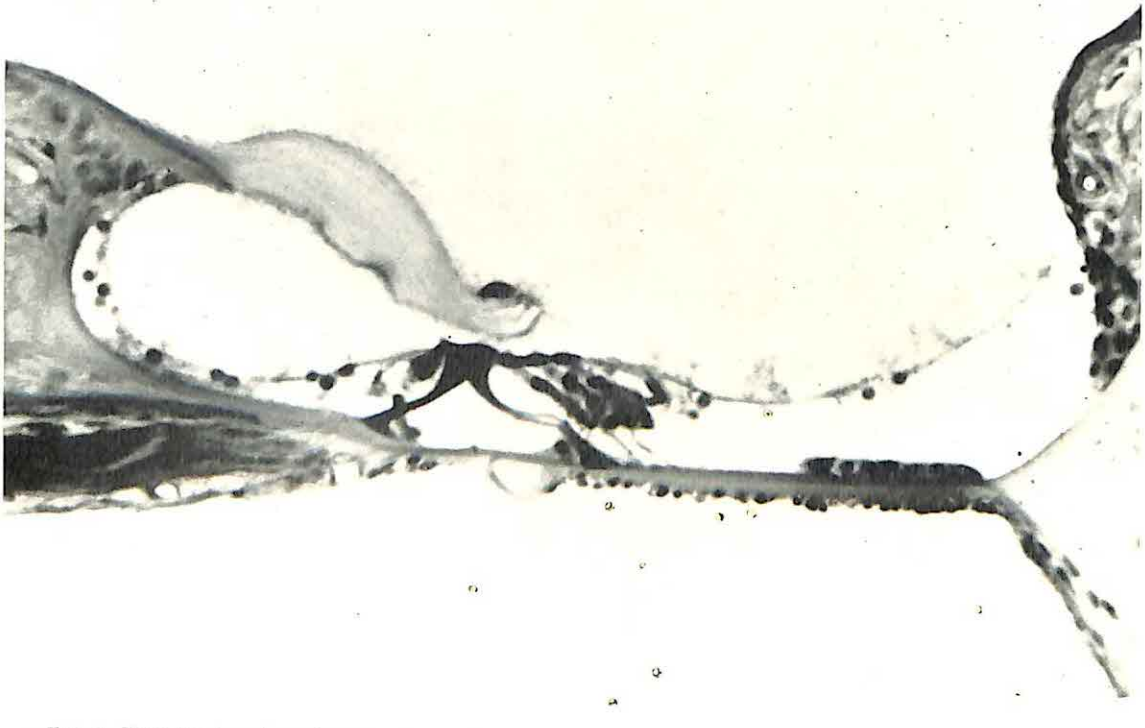

FIG. 4. Damage to external supporting cells found in some cochleas after exposure to blast stimulation

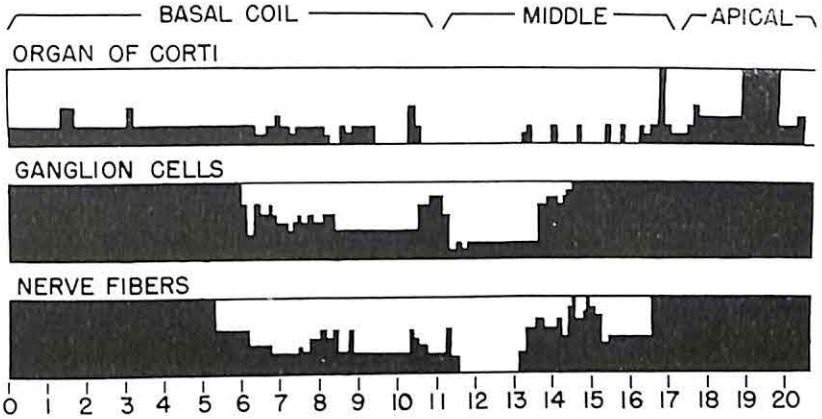

FIG. 5. Plots of hair-cell, ganglion-cell, and nerve-fiber degeneration found in the cochlea of cat 3 after blast stimulation. Normal structures are indicated by the filled-in black portion of the plots. The scale at the bottom of the figure gives the distance in millimeters from the round window.

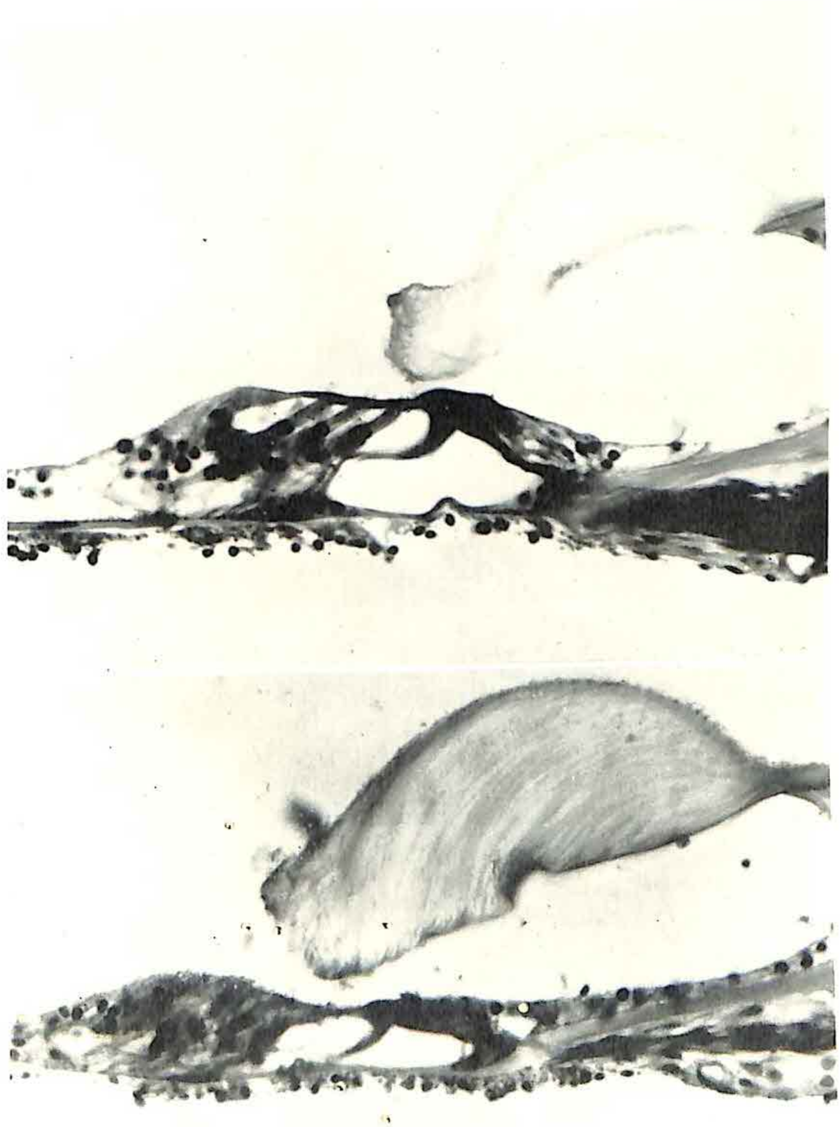

FIG. 6. Above: organ of Corti of normal cochlea. Below: organ of Corti of cat exposed to blast stimulation showing distorted appearance of hair cells which may be indicative of slight permanent damage.

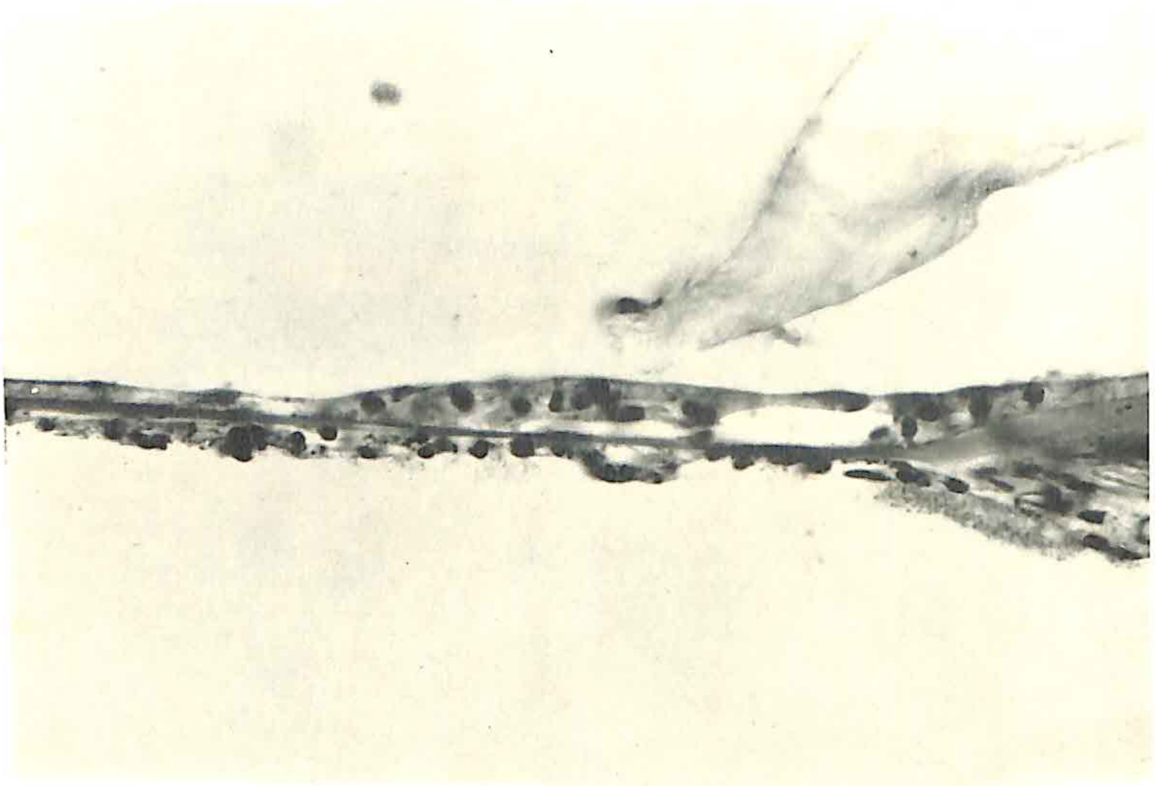

FIG. 7. Severe damage to organ of Corti of cat exposed to blast stimulation

of the histological procedure; such changes do sometimes appear in normal cochleas as a result of overperfusion with physiological saline. The limitation of the area of cell disruption to a particular region of the cochlea suggests, however, that the damage was produced by the blast stimulation.

The sections of the cochlea of cat 7, which suffered a severe hearing loss for frequencies above 2000 c.p.s., were torn in cutting so that it was impossible to make accurate estimates of the damage to the organ of Corti. The outer hair cells and supporting cells appeared to have been damaged in the middle and upper parts of the basal turn.

The most severe damage was found in the cochlea of cat 3, which also suffered the greatest loss of hearing. Plots of hair-cell destruction and nerve degeneration for the inner ear of this animal are shown in Figure 5. Outer hair cells were absent throughout the cochlea except for a region about 1 mm. in length near the apex; in this region (19 to 20 mm. on plot, Fig. 5), the outer hair cells could be seen, but they were distorted and did not appear as well defined as in the typical normal ear (see Fig. 6).

In the upper basal and lower middle turns of the cochlea of cat 3, i.e., in a region extending from about 8 mm. to 15 mm. from the basal end of the cochlea, the organ of Corti was completely demolished and appeared as a flattened lump of debris on the basilar membrane (see Fig. 7).

It may also be noted from the plots of Figure 5 that there was considerable degeneration of neural elements in the cochlea of cat 3. Ganglion cells and the peripheral nerve fibers to the hair cells were estimated as present in normal amount only in the first 5 mm. of the basal turn and in the apical region where the questionable outer hair cells were found. In the part of the cochlea where destruction of the organ of Corti was most severe, there was almost complete absence of ganglion cells in some sections.

SUMMARY AND DISCUSSION

In the cat as in man, after exposure to wide-band noise at high intensity or to explosive sounds such as produced by small arms fire, the frequency range for which hearing losses occur is centered around 4000 c.p.s. and extends one or two octaves above and below this frequency depending upon the degree of exposure. When the hearing loss is permanent and severe, degeneration of sensory cells in the upper basal and lower middle turns of the cochlea may be found upon post-mortem histological examination. When hearing losses are less severe (30 to 40 db or less), clear damage to sensory elements in the cochlea cannot always be detected. Some disruption of supporting cells of the organ of Corti may occur and the hair cells may appear slightly distorted and less well defined than in the normal ear.

In a study of the ears of guinea pigs subjected to acoustic trauma, Lurie *et al.* pointed out that "the minimum lesion that can be demonstrated, though subject to individual interpretation, is shown by changes occurring in the protoplasm of the external hair cells" (4, p. 377). He added that the changes are so indefinite that it is difficult to use them as the basis for plotting extent of damage in a cochlea. More sensitive indicators of histological changes are needed in order that inner ear dysfunction produced by trauma may be evaluated more accurately.

Complete recovery of hearing may occur in the cat after losses as great as 80 db; the time required for recovery is usually 48 hr. or less. Similar results have been reported for man by Davis *et al.* (1).

In the present study, individual differences were not systemically studied, but the evidence obtained suggests that there is considerable variability among animals in susceptibility to and recovery from temporary and permanent hearing losses which may be produced by intense acoustic stimuli.

From a practical standpoint, a most important problem is to determine the effects of repeated exposures to sounds which do not produce permanent damage to the ear at a single exposure. The fact that we have in the clinical literature such terms as "boiler-maker's deafness" and "aviator's notch" is in itself evidence that permanent hearing losses are common in occupations where repeated exposure to high noise levels occurs. But we do not know whether the losses are the result of repeated exposure to sounds at a "sub-damaging" level or of occasional exposure to peaks of sound at intensities above the ordinary level. Nor do we know how important the factor of recovery between repeated exposures is. Our experiments with cats do not provide direct evidence bearing upon these problems, but they suggest that similar intracochlear changes underlie both reversible and irreversible hearing losses.

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Received February 15, 1954.

PERFORMANCE DURING STIMULATION OF THE DIENCEPHALIC ACTIVATING SYSTEM[1]

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Recent work on the brain-stem reticular formation and other subcortical structures (Lindsley *et al.* [13, 14]; Ingram *et al.* [8, 9]; Jasper [10]) continues the work initiated by Bremer (2), whose investigations represent the first attempt to delineate the roles of these structures with respect to electrocortical and behavioral variables. Lindsley and Magoun have named certain of these structures, including the reticular formation of the mesencephalon, the posterior hypothalamus, and the mesial and intralaminar nuclei of the thalamus, the subcortical "activating system." The results of a number of current investigations (8, 9, 13, 14) are in agreement that extensive lesions in this system lead to EEG characteristics resembling those of sleep, accompanied by a striking paucity of behavior. On the other hand, stimulation in the activating system with an optimal frequency of around 300 pulses per second (16) elicits an alert EEG. In the intact animal stimulated via chronically implanted electrodes, an alert behavioral attitude, which may be described as apprehension, is often assumed. Ingram and Knott (unpublished report) have seen this alerting in waking animals during thalamic stimulation. The importance of the indicated correlation between the activity level of these diencephalic areas and gross behavior measures suggests that further definitive investigations would be advisable. The present investigation concerns itself with the effects of stimulation of certain nuclei involved in the subcortical activating system upon a quantitative measure of performance or behavior level.

METHOD

The six sexually mature cats used were chosen from stock on the basis of their friendliness and their amenability to the learning situation.

A modified Skinner box was employed which was sound shielded and contained a one-way vision glass permitting continual observation of the interior. Upon pressing a bar, the animal obtained a patty of horse meat weighing about 2 gm. A total of 24 responses per session provided the animal with 45 gm. of meat, which constituted one-half the daily meat ration. Each response actuated a recording system indicating interresponse time. The diet regimen consisted of 45 cc. of milk and 45 gm. of meat every 12 hr.

When the animal was placed in the experimental chamber for the first time, *E* operated the delivery mechanism and used such luring techniques as needed to elicit the initial bar pressing. After the animal began to make spontaneous responses, it was trained until a plateau was reached and no further significant increase in rate of responding or decrease in average interresponse time was observed.

After the animal reached the plateau in performance, stimulating electrodes were implanted in the desired nucleus. With the animal under Nembutal anesthesia, insulated nichrome steel wires were inserted under aseptic conditions with the Horsley-Clarke stereotaxic instrument. The atlases of Ajmon-Marsan and Jasper[3] and of Jimenez-Castellanos (11) were of aid in the preliminary localization of all placements. The stimulating electrodes, after insertion, were securely cemented within a plastic plug which had been screwed through the skull; knobs of solder were then fixed to the electrodes, and imbedded in the plug. Wires leading from a Grass 3 C stimulator could then be secured to these. All subsequent sessions were conducted with the stimulating wires attached. The animals did not seem aware of the presence of the plug and soon adapted to the wires, which were suspended from above the animal.

The postoperative course of each animal was generally uneventful, except that in two instances penicillin was given to forestall the effects of upper respiratory infection. When the animals had recovered sufficiently to eat all the daily ration immediately on presentation, they were again placed in the bar-pressing situation. Critical testing was carried out when preoperative performance had been approximated. It is to be noted that up to 20 days were required for recovery of preoperative performance. Tests were carried out after 6 hr. of food deprivation; this length of deprivation was used in order to allow for the exhibition of either an increase or a decrease in rate of response with "activating system" stimulation.

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[1] This is the substance of a dissertation submitted to the Psychology Department, Graduate College, State University of Iowa, in partial fulfillment of the requirements for the Doctor of Philosophy degree. The author is deeply indebted to Dr. W. R. Ingram for his services in performing the operations and in the histological evaluation of the material, and to Dr. J. R. Knott for his suggestions, help, and encouragement during the course of the experiment and the writing of this paper.

[2] Now at Aeromedical Laboratory, Wright Air Development Center, Dayton, Ohio.

[3] AJMON-MARSON, C., & JASPER, H. H. Stereotoxic atlas of the cat diencephalon. Privately circulated manuscript.

The stimulator was set to deliver a series of biphasic pulses, each with a duration of 1 msec. The leads from the stimulator to the animal were secured to the previously described solder knobs using an instrument-type soldering iron. The frequency of the pulses in all experiments here reported was 300 biphasic pulses per sec. Other frequencies, higher and lower, were tried, but any wide deviation from 300 per sec. did not produce the results to be described. The actual voltage used varied from animal to animal, and in some animals, from day to day. The voltage chosen was that just below the level needed to evoke some overt response, usually a searching attitude or in some cases pupillary dilatation or slight skeletal muscle response. (The voltages given in Table 1 were determined from calibration with an oscilloscope; the "dial voltages" of the stimulator were slightly higher.)

On alternate days the animal received the stimulation pulses throughout the time it was in the response situation. On the other days no stimulus was applied, although the wires were routinely attached.

At the conclusion of the training series, the animals were sacrificed, the brains removed, fixed, and frozen sections made. Exact histological verification of each placement was available, and the presumed location, based on the Horsley-Clarke coordinates, verified. No damage was observed in any of the brains other than that damage attendant upon the introduction of the needle electrode itself.

RESULTS

The basic data are summarized in Table 1. It will be seen that the rate of responding was slowed on those days when the stimulation was introduced. In addition, with the exception of one animal (StL4) on one comparison (first), the variances were greater under stimulation. This occurred with each of the three placements: the *nucleus ventromedialis; centrum medianum* of the thalamus; and the posterior hypothalamus.

The means (paired days) were compared with the t test for related measures, which requires no assumption about the variance or distribution of the two arrays, and in all but one animal ($p = .02$) the differences were significant at better than the 1 per cent level of confidence. These differences were uniformly in the direction of a decrease in the rate of bar pressing as a result of the introduction of the 300-per-sec. biphasic pulse stimulus into the diffuse projection system or the brain stem reticular system of the respective animals. With the stimulus parameters used, stimulation did not produce the total blocking response observed by Hunter and Jasper (7).

TABLE 1

Location of Electrode, Stimulus Voltage, and Mean Time (in seconds) between Responses for Stimulation and Nonstimulation Days

($N = 24$ for each mean)

Animal	Stimulus Location	Volts	Stimulation		Nonstimulation	
			Mean	Variance	Mean	Variance
StL3	Posterior hypothalamus	3.0	12.13	15.22	9.23	10.55
		3.0	11.66	9.33	9.30	7.33
		3.0	10.95	11.33	8.65	5.78
		2.7	9.58	7.89		
		2.7	9.68	7.58		
StL4	*Nucleus ventromedialis* thalamus	3.0	7.81	2.83	6.70	5.68
		3.0	6.71	8.28	6.06	2.17
		3.5	5.75	10.58	4.83	1.89
		3.5	5.61	2.55	4.90	1.58
		4.0	9.40	19.55	6.56	1.67
		4.0	7.00	19.02	5.31	7.30
		4.0	7.40	15.41	4.63	0.58
		4.0	9.56	72.20	4.28	1.28
StL6	*Nucleus ventromedialis* thalamus	8.0	8.13	5.78	7.58	1.89
		9.25	7.60	5.44	6.69	3.03
		9.25	7.80	2.75	7.08	2.00
StL7	*Nucleus ventromedialis* thalamus	5.5	8.30	10.44	7.63	2.72
		5.5	7.05	3.39	6.31	1.61
		5.5	6.43	3.44	5.01	1.58
		5.5	5.69	11.80	4.78	0.50
StL8	*Nucleus ventromedialis* thalamus	4.0	9.38	10.25	7.90	3.78
		4.0	7.70	5.17	6.75	2.50
		4.0	8.01	10.16	6.73	2.75
		3.5	7.76	7.69	6.51	4.50
StL9	*Centrum medianum*	4.5	6.15	4.64	4.78	1.25
		4.5	7.33	5.17	5.93	2.11
		4.5	7.05	3.94	6.03	2.89

DISCUSSION

Material such as that presented in the introduction of this paper has led Lindsley (12) to suggest that the emotional level of the organism is closely related to, if not dependent upon, the level of activity of the midbrain activating system. Within this context, then, it might be said that the results of the present experiment are more in line with the thinking of those who take the position that increased motivation or emotion produces more variable but not a higher level of performance, as opposed to the position that increased motivation increases reaction potential. The increased variability noted under the stimulation condition also tends to support the former position. However, the framework of the present experiment does not provide a clear-cut decision as to the behavioral nature of diencephalic stimulation. If one were to take seriously the notion that the animals exhibit an "apprehensive attitude" under stimulation and, therefore, assume that the stimulation has effects analogous to those of anxiety, the experimental results resemble the slower rate of bar pressing which Estes and Skinner (4) found in rats under shock-induced anxiety. Considering, in addition, the observable unconditioned responses to diencephalic stimulation, the present results can thus be explained (following Estes and Skinner) in terms of the introduction of irrelevant responses. The irrelevant response notion is also indicated by the increased variability. The employment of the startle response (3) would provide a test of this explanation.

The results could be considered independently of the suggested motivational properties of the stimulation. Namely, it could be argued that the introduction of stimulation resulted in an alteration of the learning situation (prestimulation) stimulus complex. This argument would imply that there were sensory "consequences" of the stimulation, which implication is contrary to the findings of White (19), who states that there were no reports in the usual sense of sensations by humans during stimulation of the hypothalamus under local anesthesia. If there were *sensory* consequences of diencephalic stimulation in the regions studied here, such stimulation could be used as the conditioned stimulus in a classical conditioning situation, thus providing a test of this notion.

Schreiner *et al.* (17), since the completion of this study, have published the results of a study which indicate that complete bilateral destruction of the *nucleus dorsalis medialis* thalami in the cat leads to an inability to learn in a problem box. This result further points out the significance of the diencephalic region to behavior.

SUMMARY

1. Six animals were trained on a bar-pressing response with food reward to a criterion of no further improvement in performance.

2. Electrodes were implanted stereotaxically by the Horsley-Clarke method; the electrodes were in the posterior hypothalamus in one animal, the ventromedial thalamic nucleus in four animals, and the *centrum medianum* of the thalamus in one animal.

3. The animals were tested with respect to rate of responding under stimulation and nonstimulation conditions. The animals responded more slowly and with greater variability under stimulation.

4. It is concluded that stimulation of the diencephalon serves as a distracting influence on rate of responding under the conditions of the present study. It is suggested that the production of minimally observable extraneous responses is most acceptable as a possible explanation of the obtained results.

5. Further ways of experimentally attacking the problem are suggested.

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Received January 26, 1954.

SOME POSITIVE RESULTS ON A MODIFIED TOLMAN AND HONZIK INSIGHT MAZE

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The problem of investigating insight in animals suggested the present study patterned on an experiment performed by Tolman and Honzik (7). The experiment was designed to show whether or not rats were capable of grasping "a material, inner relation of two things to each other"; specifically, it was to discover whether a rat can get the "insight" that two paths have a common section.

In general, the evidence for insight in rats is negative, and Evans (1) and Keller and Lyndon (4) question the use of the term in the Tolman-Honzik type of experiment. Kuo (5), who used a different type of design from that employed by Tolman and Honzik, also opposes the use of the concept.

Tolman and Honzik actually did three experiments. Owing to negative results on the first maze, they decided to try a maze in which the choice between paths 2 and 3 would require larger movement, that is, a turning through 90° to right or left. Because the results were still negative after this second experiment, they decided to try a third, elevated-type maze. The results of the third experiment are considered significant by them.

In the present study, the second experiment will be investigated further rather than the third because in the third experiment the animal might see the whole experiment, thus placing the results within the area of perception rather than insight (2, 6).

In Tolman and Honzik's second experiment, a closed maze made up of three pathways leading to a goal is used. The first path is straight and leads directly to the goal; the second path is more roundabout—toward the end it joins path 1; the third is much longer than the other two pathways, and separate. When path 1 is blocked at the entrance, path 2 will allow the rat to reach the goal, but if path 1 is blocked toward the end of the pathway, where path 2 has already merged with it, only path 3 is left free. In the preliminary training, the "forced" runs were blocked at the entrance to path 1, permitting a choice of path 2 or 3. In the "insight" runs, however, path 1 was blocked toward the end of the path after path 2 had joined it, thus leaving only path 3 free to the goal. The independent variable is the blocking of paths 1 and 2 on the insight runs, and the dependent variable is the reaction of the rats to this change in blocking.

The present problem is to investigate the introduction of an elevated cue, a curved piece of hardware cloth covered with sandpaper placed at the junction of paths 1 and 2 of the maze, to see if this would aid the animals in grasping the relationship that path 2 is blocked when path 1 is blocked, and result in their choosing path 3.

METHOD

Subjects

This experiment was performed on two groups of rats, with 10 rats in group I and 11 in group II. Three-month-old albino males, from Carworth Farms, New City, New York, were used.

Apparatus

The apparatus (see Fig. 1) was similar to Tolman and Honzik's maze in their second experiment, with the addition of an elevated cue at the junction of paths 1 and 2. The maze was constructed of pine and plywood, and painted black. The alleys were 4 in. wide, and the walls were 6 in. high. The tops of the alleys were covered with ½-in. mesh hardware cloth. Gates were pivoted at the bottom and slanted upward away from the rat. The upper edges of the gates were held by rubber bands against the covers of the alleys, and the tension was such that the rat by stepping on a gate would, by the force of its weight, be able to push the gate down and pass over it. Once *S* was through, the gate would swing up behind it and prevent retracing. The entrance to each path could be closed by a sliding door made of beaver board.

The cue was a curved piece of hardware cloth covered with sandpaper inserted at the junction of paths 1 and 2 to cause an elevation and a different texture at that point. It was as wide as the pathway, and curved in such a way that the rat had to run up one side and down the other side of the cue to the normal surface of the pathway.

Procedure

Preliminary training. The rats were given ten runs a day for 13 days. For the first two days, the first three

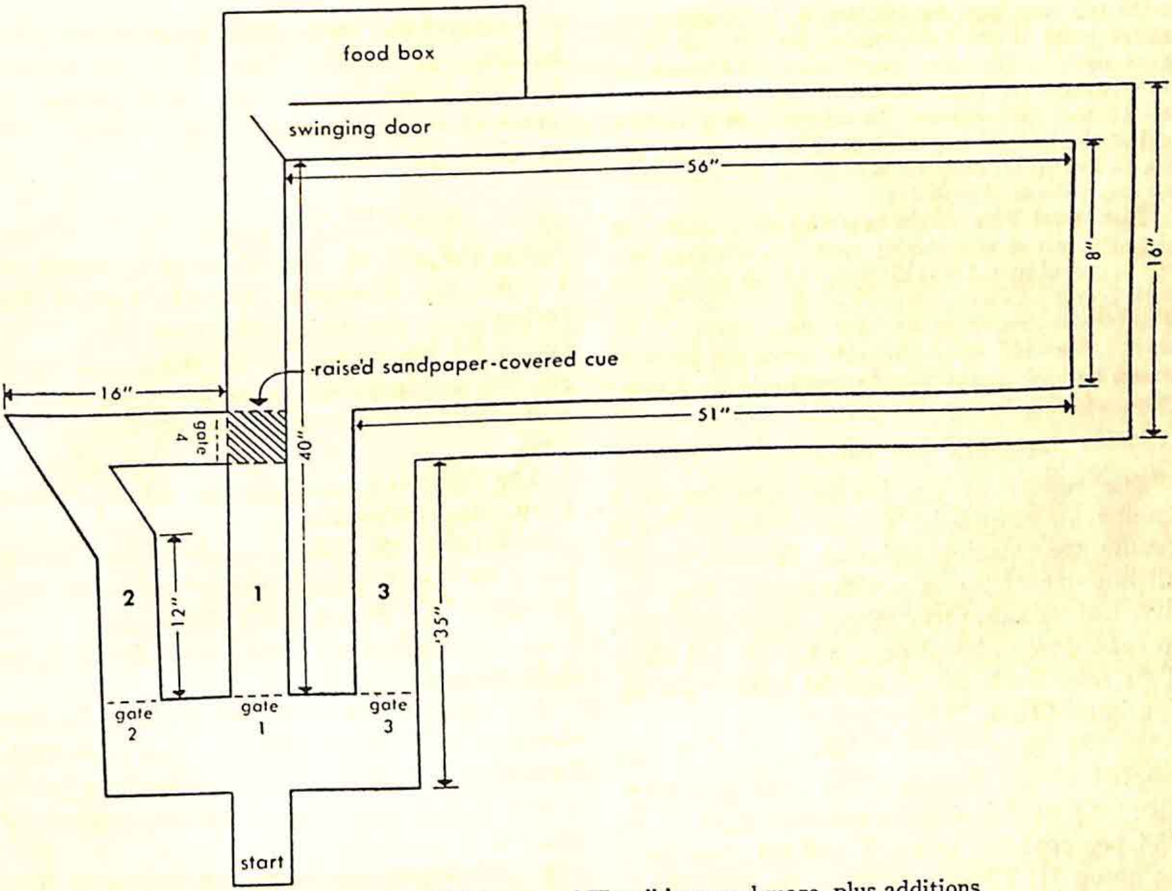

FIG. 1. Floor plan of Tolman and Honzik's second maze, plus additions

TABLE 1

Choice of Paths on Insight Runs—Group I

Rat	1		2		3		4		5		6		7		8		9		10	
Paths	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3
Runs																				
1		×		×		×		×		×		×		×	×			×		×
2		×	×			×		×		×	×		×			×	×			×
3		×		×		×		×		×		×		×		×	×		×	
4	×			×		×	×			×		×	×			×		×	×	
5		×		×		×		×		×	×			×		×		×		×

TABLE 2

Choice of Paths on Insight Runs—Group II

Rat	1		2		3		4		5		6		7		8		9		10		11	
Paths	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3
Runs																						
1	×			×		×		×		×		×		×		×		×		×		×
2	×			×		×		×		×	×		×		×		×			×		×
3	×			×		×		×		×		×	×			×		×		×		×
4		×		×		×	×		×		×			×		×		×		×		×
5	×			×	×			×	×			×		×		×		×		×	×	

of the ten runs were forced; that is, by blocking successive pairs of the three paths, the rat was forced down each of the three paths once. The remaining seven runs were free. After two days, this type of forcing was discontinued. In the remaining training period, the method was to block path 1 at the entrance one to five times daily for a total of 32 runs, leaving the rats a choice of path 2 or 3.

Test period. Five insight runs were given on the day after the last of the training runs. The swinging door at the end of path 1 was blocked, and the two gates in path 1 were let down, permitting the animal's return. The second gate of path 2, the place where it joins path 1, was not let down; this prevented the rat's return by path 2, and *S* had to return to the starting point, and then take path 2 or 3.

RESULTS AND DISCUSSION

The results of the insight runs for both groups are shown in Tables 1 and 2. These results are amazingly similar. In each group, all but one of the rats picked path 3 on the first insight run. Over 50 per cent of the rats in each group picked path 3 the second time. Two from each group picked path 3 on all five insight runs.

On the forced runs on which path 1 was blocked at the entrance, the average preference for path 2 in comparison with path 3 was 90.8 per cent for group I and 90.4 per cent for group II. Three rats chose path 2 all the time. An interesting fact is that of these three only one picked path 2 on the first insight run.

It is significant that four rats chose path 3 every time on the insight runs, especially as their average preference for path 2 on the blocked runs was over 90 per cent. A comparison between the performance on the first trial in the training series for which gate 1 was blocked at the entrance and the performance on the first insight trial showed that on the former no animal in group I chose path 3 and 18 per cent in group II chose path 3, whereas on the latter 90 per cent of group I chose path 3 and 91 per cent of group II chose path 3.

If insight is defined as one-trial learning which is subsequently maintained, then this definition is not applicable here, as the data indicate a sharp loss in performance on trial 2 and subsequent trials. This necessitates a redefinition of insight. These data also suggest that the performance might be explained in terms of other concepts such as Hull's (3) reactive inhibition.

SUMMARY AND CONCLUSIONS

The purpose of this experiment, based on Tolman and Honzik's "insight in rats" experiment, was to see if introducing an elevated cue at the intersection of paths 1 and 2 would aid the rats in grasping the fact that paths 1 and 2 had a common section leading to the goal.

The following conclusions may be drawn from this experiment:

1. On the first insight run 19 of the 21 rats chose path 3, although over 90 per cent had chosen path 2 on the forced runs.
2. Four rats chose path 3 on all five insight runs.
3. The results suggest that the introduction of a cue into Tolman and Honzik's maze may have aided the animals in grasping that paths 1 and 2 have a common section leading to the goal.
4. This experiment supports Tolman's conception of insight or inference as he used the term in his experiment, i.e., as perceptual organization that occurs when the total situation is not present.

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Received February 3, 1954.

POSITIVE REINFORCEMENT PRODUCED BY ELECTRICAL STIMULATION OF SEPTAL AREA AND OTHER REGIONS OF RAT BRAIN[1]

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Stimuli have eliciting and reinforcing functions. In studying the former, one concentrates on the responses which come after the stimulus. In studying the latter, one looks mainly at the responses which precede it. In its reinforcing capacity, a stimulus increases, decreases, or leaves unchanged the frequency of preceding responses, and accordingly it is called a reward, a punishment, or a neutral stimulus (cf. 16).

Previous studies using chronic implantation of electrodes have tended to focus on the eliciting functions of electrical stimuli delivered to the brain (2, 3, 4, 5, 7, 10, 12, 14). The present study, on the other hand, has been concerned with the reinforcing function of the electrical stimulation.[3]

METHOD

General

Stimulation was carried out by means of chronically implanted electrodes which did not interfere with the health or free behavior of *S*s to any appreciable extent. The *S*s were 15 male hooded rats, weighing approximately 250 gm. at the start of the experiment. Each *S* was tested in a Skinner box which delivered alternating current to the brain so long as a lever was depressed. The current was delivered over a loose lead, suspended from the ceiling, which connected the stimulator to the rat's electrode. The *S*s were given a total of 6 to 12 hr. of acquisition testing, and 1 to 2 hr. of extinction testing. During acquisition, the stimulator was turned on so that a response produced electrical stimulation; during extinction, the stimulator was turned off so that a response produced no electrical stimulation. Each *S* was given a percentage score denoting the proportion of his total acquisition time given to responding. This score could be compared with the animal's extinction score to determine whether the stimulation had a positive, negative, or neutral reinforcing effect. After testing, the animal was sacrificed. Its brain was frozen, sectioned, stained, and examined microscopically to determine which structure of the brain had been stimulated. This permitted correlation of acquisition scores with anatomical structures.

Electrode Implantation

Electrodes are constructed by cementing a pair of enameled silver wires of 0.010-in. diameter into a Lucite block, as shown in Figure 1. The parts of the wires which penetrate the brain are cemented together to form a needle, and this is cut to the correct length to reach the desired structure in the brain. This length is determined from Krieg's rat brain atlas (11) with slight modifications as found necessary by experience. The exposed cross section of the wire is the only part of the needle not insulated from the brain by enamel; stimulation therefore occurs only at the tip. Contact with the lead from the stimulator is made through two blobs of solder on the upper ends of the electrode wires; these blobs make contact with the jaws of an alligator clip which has been modified to insulate the two jaws from one another. A light, flexible hearing-aid lead connects the clip to the voltage source.

The operation of implantation is performed with the rat under Nembutal anesthesia (0.88 cc/Kg) and held in a Johnson-Krieg stereotaxic instrument (11). A mid-line incision is made in the scalp and the skin held out of the way by muscle retractors. A small hole is drilled in the skull with a dental burr at the point indicated by the stereotaxic instrument for the structure it is desired to stimulate. The electrode, which is clamped into the needle carrier of the instrument, is lowered until the flange of the Lucite block rests firmly on the skull. Four screw holes are then drilled in the skull through four fixing holes in the flange, and the electrode, still clamped firmly in the instrument, is fastened to the skull with jeweler's screws which exceed the diameter of the screw holes in the skull by 0.006 in. The electrode is then released from the clamp and the scalp wound closed with silk sutures. The skin is pulled tightly around the base of the Lucite block and kept well away from the contact plates. A recovery period of three days is allowed after the operation before testing. Figure 2 is an X-ray picture of an electrode in place.

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[1] The research reported here was made possible by grants from the Rockefeller Foundation and the National Institute of Mental Health of the U.S. Public Health Service. The authors particularly wish to express their thanks to Professor D. O. Hebb, who provided germinal ideas for the research and who backed it with enthusiastic encouragement as well as laboratory facilities and funds. The authors are also grateful to Miss Joann Feindel, who performed the histological reconstructions reported here.

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[3] The present preliminary paper deals mainly with methods and behavioral results. A detailed report of the locus of positive, negative, and neutral reinforcing effects of electrical brain stimulation is being prepared by the first author.

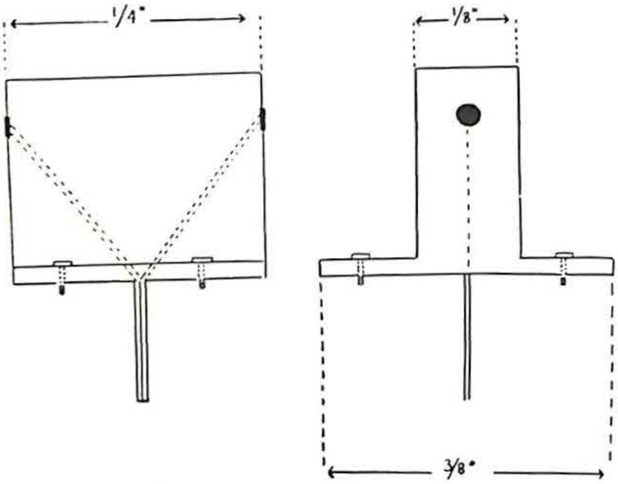

FIG. 1. Electrode design (see text for detailed description)

Testing

The testing apparatus consisted of a large-levered Skinner box 11 in. long, 5 in. wide, and 12 in. high. The top was open to allow passage for the stimulating lead. The lever actuated a microswitch in the stimulating circuit so that when it was depressed, the rat received electrical stimulation. The current was obtained from the 60-cycle power line, through a step-down transformer, and was adjustable between 0 and 10 v. r.m.s. by means of a variable potentiometer. In the experiments described here the stimulation continued as long as the lever was pressed, though for some tests a time-delay switch was incorporated which cut the current off after a predetermined interval if the rat continued to hold the lever down. Responses were recorded automatically on paper strip.

On the fourth day after the operation rats were given a pretesting session of about an hour in the boxes. Each rat was placed in the box and on the lever by *E* with the stimulus set at 0.5 v. During the hour, stimulation voltage was varied to determine the threshold of a "just noticeable" effect on the rat's behavior. If the animal did not respond regularly from the start, it was placed on the lever periodically (at about 5-min. intervals). Data collected on the first day were not used in later calculations. On subsequent days, *S*s were placed in the box for about 3½ hr. a day; these were 3 hr. of acquisition and ½ hr. of extinction. During the former, the rats were allowed to stimulate themselves with a voltage which was just high enough to produce some noticeable response in the resting animal. As this threshold voltage fluctuated with the passage of time, *E* would make a determination of it every half hour, unless *S* was responding regularly. At the beginning of each acquisition period, and after each voltage test, the animal was placed on the lever once by *E*. During extinction periods, conditions were precisely the same except that a bar press produced no electrical stimulation. At the beginning of each extinction period, animals which were not responding regularly were placed on the lever once by *E*. At first, rats were tested in this way for four days, but as there appeared to be little difference between the results on different days, this period was reduced to three and then to two days for

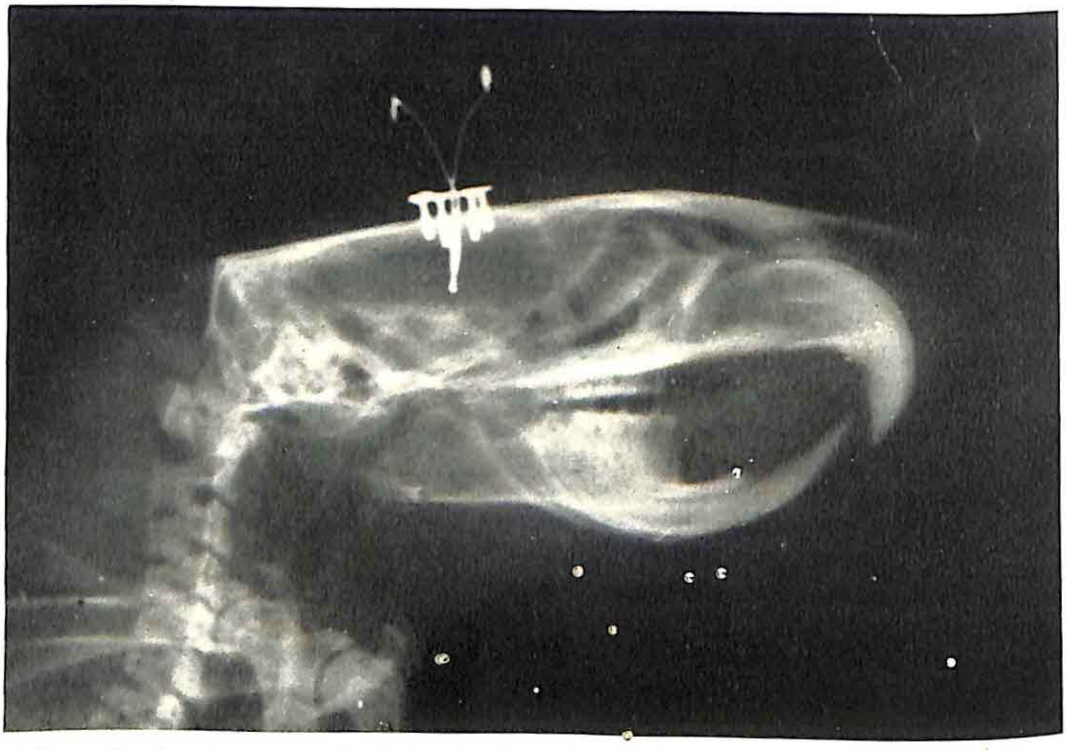

FIG. 2. X ray showing electrode in place in intact animal. There are two wires insulated completely from each other, stimulating the brain with their tips.

subsequent animals. Thus, the first rats had about 12 hr. of acquisition after pretesting whereas later rats had about 6 hr. However, in computing the scores in our table, we have used only the first 6 hr. of acquisition for all animals, so the scores are strictly comparable. In behavioral curves, we have shown the full 12 hr. of acquisition on the earlier animals so as to illustrate the stability of the behavior over time.

At no time during the experiment were the rats deprived of food or water, and no reinforcement was used except the electrical stimulus.

Animals were scored on the percentage of time which they spent bar pressing regularly during acquisition. In order to find how much time the animal would spend in the absence of reward or punishment, a similar score was computed for periods of extinction. This extinction score provided a base line. When the acquisition score is above the extinction score, we have reward; when it is below the extinction score, we have punishment.

In order to determine percentage scores, periods when the animal was responding regularly (at least one response every 30 sec.) were counted as periods of responding; i.e., *intervals of 30 sec. or longer without a response were counted as periods of no responding.* The percentage scores were computed as the proportion of total acquisition or extinction time given to periods of responding.

Determination of Locus

On completion of testing, animals were perfused with physiological saline, followed by 10 per cent formalin. The brains were removed, and after further fixation in formalin for about a week, frozen sections 40 microns thick were cut through the region of the electrode track. These were stained with cresyl violet and the position of the electrode tip determined. Figure 3 is a photomicrograph showing the appearance of the electrode track in a stained and mounted brain section.

RESULTS

Locus

In Table 1, acquisition and extinction scores are correlated with electrode placements.

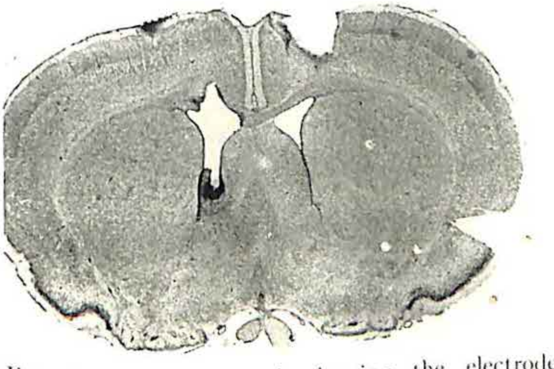

FIG. 3. Photomicrograph showing the electrode track in a cresyl-violet stained brain section. The section is 1 mm. in front of the anterior commissure. The electrode protruded through the lateral ventricle and its stimulating tip was in the septal area.

TABLE 1

Acquisition and Extinction Scores for All Animals Together with Electrode Placements and Threshold Voltages Used during Acquisition Tests

Animal's No.	Locus of Electrode	Stimulation Voltage r.m.s.	Percentage of Acquisition Time Spent Responding	Percentage of Extinction Time Spent Responding
32	septal	2.2–2.8	75	18
34	septal	1.4	92	6
M-1	septal	1.7–4.8	85	21
M-4	septal	2.3–4.8	88	13
40	c.c.	.7–1.1	6	3
41	caudate	.9–1.2	4	4
31	cingulate	1.8	37	9
82	cingulate	.5–1.8	36	10
36	hip.	.8–2.8	11	14
3	m.l.	.5	0	4
A-5	m.t.	1.4	71	9
6	m.g.	.5	0	31
11	m.g.	.5	0	21
17	teg.	.7	2	1
9	teg.	.5	77	81

KEY: *c.c.*, *corpus callosum; hip.*, hippocampus; *m.l.*, medial lemniscus; *m.t.*, Mammillothalamic tract; *m.g.*, medial geniculate; *teg.*, tegmentum.

Figure 4 presents the acquisition scores again, this time on three cross-sectional maps of the rat brain, one at the forebrain level, one at the thalamic level, and one at the mid-brain level. The position of a score on the map indicates the electrode placement from which this acquisition score was obtained.

The highest scores are found together in the central portion of the forebrain. Beneath the *corpus callosum* and between the two lateral ventricles in section I of Figure 4, we find four acquisition scores ranging from 75 to 92 per cent. This is the septal area. The *S*s which produced these scores are numbered 32, 34, M-1, and M-4 in Table 1. It will be noticed that while all of them spent more than 75 per cent of their acquisition time responding, they all spent less than 22 per cent of their extinction time responding. Thus the electrical stimulus in the septal area has an effect which is apparently equivalent to that of a conventional primary reward as far as the maintenance of a lever-pressing response is concerned.

If we move outside the septal area, either in the direction of the caudate nucleus (across the lateral ventricle) or in the direction of the *corpus callosum*, we find acquisition scores drop abruptly to levels of from 4 to 6 per cent. These are definitely indications of neutral (neither rewarding nor punishing) effects.

However, above the *corpus callosum* in the cingulate cortex we find an acquisition score of 37 per cent. As the extinction score in this case was 9 per cent, we may say that stimulation was rewarding.

At the thalamic level (section II of Fig. 4) we find a 36 per cent acquisition score produced by an electrode placed again in the cingulate cortex, an 11 per cent score produced by an electrode placed in the hippocampus, a 71 per cent score produced by an electrode placed exactly in the mammillothalamic tract, and a zero per cent score produced by an electrode placed in the medial lemniscus. The zero denotes negative reinforcement.

At the mid-brain level (section III of Fig. 4) there are two zero scores produced by electrodes which are in the posterior portion of the medial geniculate bodies; here again, the scores indicate a negative effect, as the corresponding extinction scores are 31 and 21 per cent. There is an electrode deep in the medial, posterior tegmentum which produces a 2 per cent score; this seems quite neutral, as the extinction score in this case is 1 per cent.

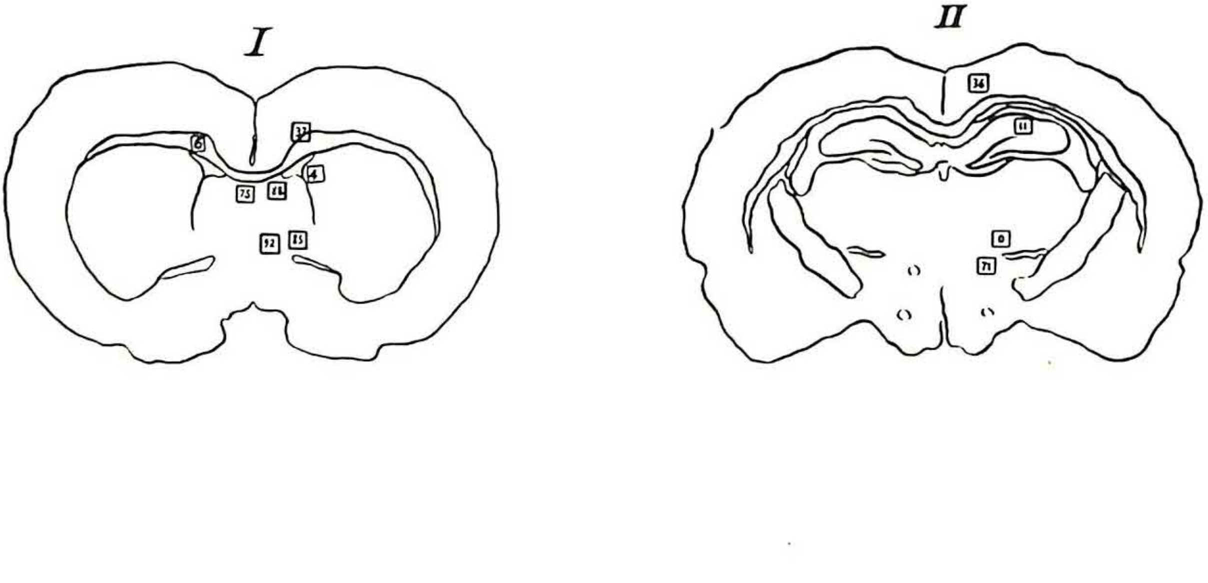

FIG. 4. Maps of three sections, (I) through the forebrain, (II) through the thalamus, (III) through the mid-brain of the rat. Boxed numbers give acquisition percentage scores produced by animals with electrodes stimulating at these points. On section I the acquisition scores 75, 88, 92, 85 fall in the septal forebrain area. On the same section there is a score of 4 in the caudate nucleus, a score of 6 in the white matter below the cortex, and a score of 37 in the medial (cingulate) cortex. On section II the acquisition score of 36 is in the medial (cingulate) cortex, 11 is in the hippocampus, 71 is in the mammillothalamic tract, and 0 is in the medial lemniscus. On section III the two zeroes are in the medial geniculate, 2 is in the tegmental reticular substance, 77 falls 2 mm. anterior to the section shown it is between the posterior commissure and the red nucleus.

Finally, there is an electrode shown on this section which actually stands 1½ mm. anterior to the point where it is shown; it was between the red nucleus and the posterior commissure. It produced an acquisition score of 77 per cent, but an extinction score of 81 per cent. This must be a rewarding placement, but the high extinction score makes it difficult to interpret.

Behavior

We turn our attention briefly to the behavioral data produced by the more rewarding electrode placements.

The graph in Figure 5 is a smoothed cumulative response curve illustrating the rate of responding of rat No. 32 (the lowest-scoring septal area rat) during acquisition and extinction. The animal gave a total of slightly over 3000 responses in the 12 hr. of acquisition. When the current was turned on, the animal responded at a rate of 285 responses an hour; when the current was turned off, the rate fell close to zero.

The graph in Figure 6 gives similar data on rat No. 34 (the highest-scoring septal rat). The animal stimulated itself over 7500 times in 12 hr. Its average response rate during acquisition was 742 responses an hour; during extinction, practically zero.

Figure 7 presents an unsmoothed cumulative response curve for one day of responding

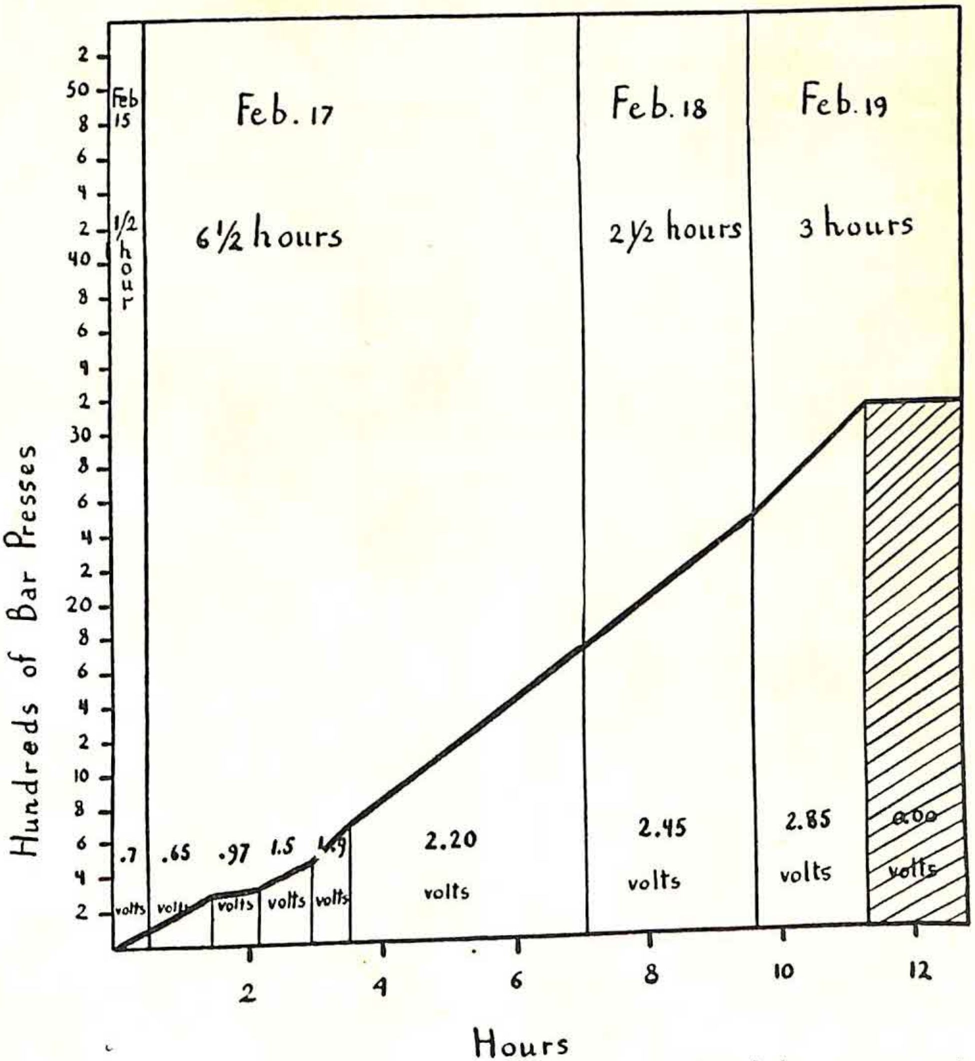

FIG. 5. Smoothed cumulative response curve for rat No. 32. Cumulative response totals are given along the ordinate, and hours along the abscissa. The steepness of the slope indicates the response rate. Stimulating voltages are given between black lines. Cross hatching indicates extinction.

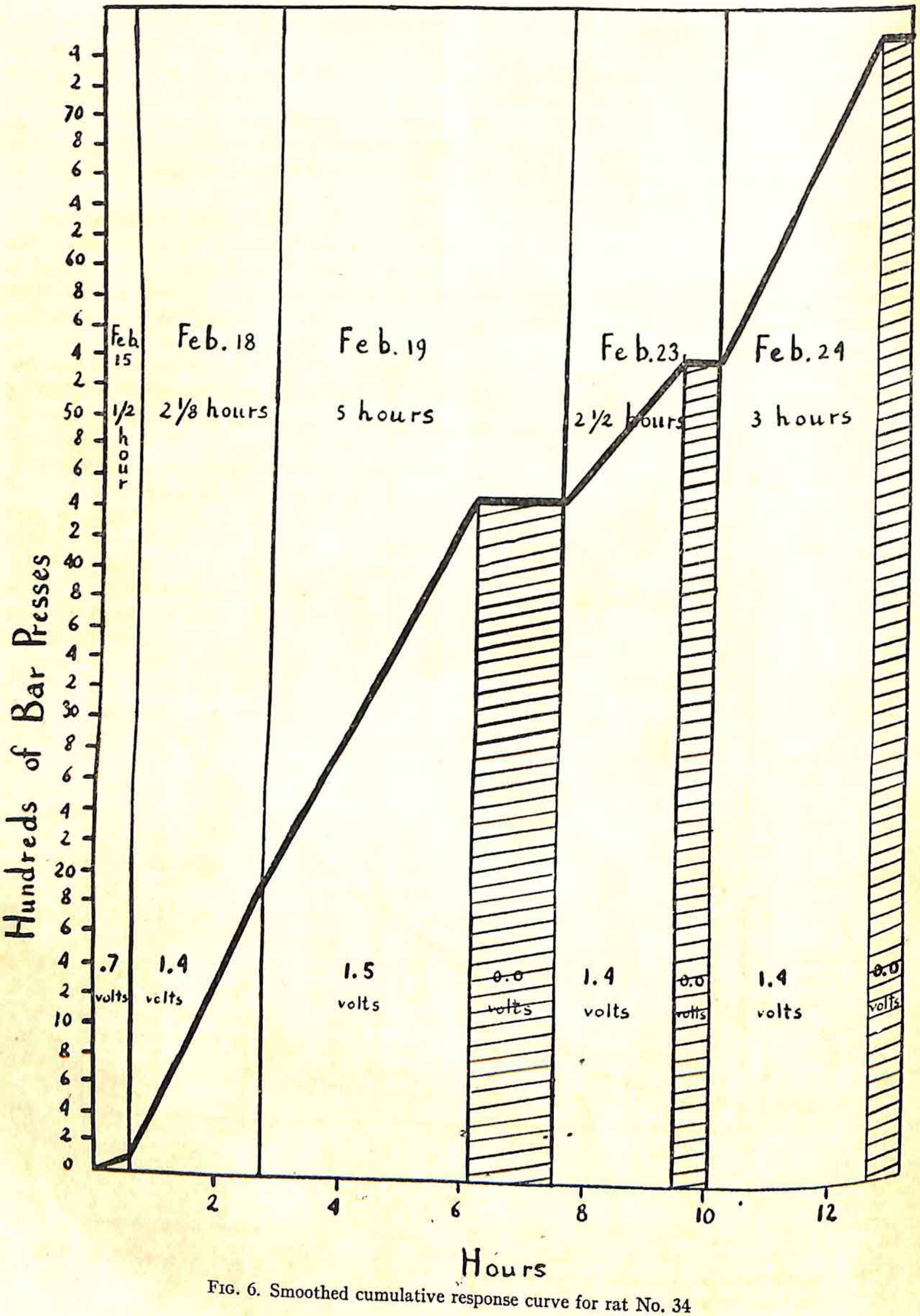

FIG. 6. Smoothed cumulative response curve for rat No. 34

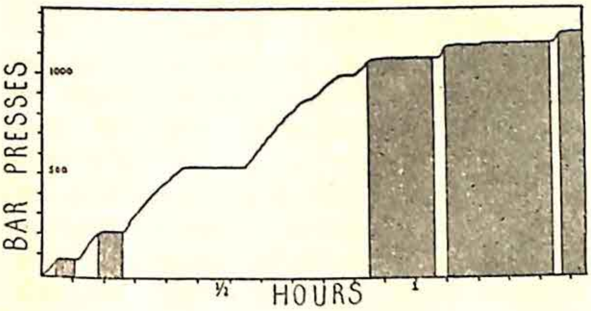

FIG. 7. Unsmoothed cumulative response curve showing about ¾ hr. of acquisition and ¾ hr. extinction for rat No. A-5. Shading indicates extinction.

for rat No. A-5. This is to illustrate in detail the degree of control exercised by the electrical reward stimulus. While this rat was actually bar pressing, it did so at 1920 responses an hour; that is, about one response for every 2 sec. During the first period of the day it responded regularly while on acquisition, extinguished very rapidly when the current was turned off, and reconditioned readily when the current was turned on again. At reconditioning points, *E* gave *S* one stimulus to show that the current was turned on again, but *E* did not place *S* on the lever. During longer periods of acquisition, *S* occasionally stopped responding for short periods, but in the long run *S* spent almost three-quarters of its acquisition time responding. During the long period of extinction at the end of the day, there was very little responding, but *S* could be brought back to the lever quite quickly if a stimulus was delivered to show that the current had been turned on again.

DISCUSSION

It is clear that electrical stimulation in certain parts of the brain, particularly the septal area, produces acquisition and extinction curves which compare favorably with those produced by a conventional primary reward. With other electrode placements, the stimulation appears to be neutral or punishing.

Because the rewarding effect has been produced maximally by electrical stimulation in the septal area, but also in lesser degrees in the mammillothalamic tract and cingulate cortex, we are led to speculate that a system of structures previously attributed to the rhinencephalon may provide the locus for the reward phenomenon. However, as localization studies which will map the whole brain with respect to the reward and punishment dimension are continuing, we will not discuss in detail the problem of locus. We will use the term "reinforcing structures" in further discussion as a general name for the septal area and other structures which produce the reward phenomenon.

To provide an adequate canvass of the possible explanations for the rewarding effect would require considerably more argument than could possibly fit within the confines of a research paper. We have decided, therefore, to rule out briefly the possibility that the implantation produces pain which is reduced by electrical stimulation of reinforcing structures, and to confine further discussion to suggestions of ways the phenomenon may provide a methodological basis for study of physiological mechanisms of reward.

The possibility that the implantation produces some painful "drive stimulus" which is alleviated by electrical stimulation of reinforcing structures does not comport with the facts which we have observed. If there were some chronic, painful drive state, it would be indicated by emotional signs in the animal's daily behavior. Our *S*s, from the first day after the operation, are normally quiet, nonaggressive; they eat regularly, sleep regularly, gain weight. There is no evidence in their behavior to support the postulation of chronic pain. Septal preparations which have lived healthy and normal lives for months after the operation have given excellent response rates.

As there is no evidence of a painful condition preceding the electrical stimulation, and as the animals are given free access to food and water at all times except while actually in the Skinner boxes, there is no explicitly manipulated drive to be reduced by electrical stimulation. Barring the possibility that stimulation of a reinforcing structure specifically inhibits the "residual drive" state of the animal, or the alternative possibility that the first electrical stimulus has noxious aftereffects which are reduced by a second one, we have some evidence here for a primary rewarding effect which is not associated with the reduction of a primary drive state. It is perhaps fair in a discussion to report the "clinical impression" of the *E*s that the phenomenon represents strong pursuit of a positive stimulus rather than escape from some negative condition.

Should the latter interpretation prove correct, we have perhaps located a system within the brain whose peculiar function is to produce a rewarding effect on behavior. The location of such a system puts us in a position to collect information that may lead to a decision among conflicting theories of reward. By physiological studies, for example, we may find that the reinforcing structures act selectively on sensory or motor areas of the cortex. This would have relevance to current S-S versus S-R controversies (8, 9, 13, 16).

Similarly, extirpation studies may show whether reinforcing structures have primarily a quieting or an activating effect on behavior; this would be relevant to activation versus negative feedback theories of reward (6, 13, 15, 17). A recent study by Brady and Nauta (1) already suggests that the septal area is a quieting system, for its surgical removal produced an extremely active animal.

Such examples, we believe, make it reasonable to hope that the methodology reported here should have important consequences for physiological studies of mechanisms of reward.

SUMMARY

A preliminary study was made of rewarding effects produced by electrical stimulation of certain areas of the brain. In all cases rats were used and stimulation was by 60-cycle alternating current with voltages ranging from ½ to 5 v. Bipolar needle electrodes were permanently implanted at various points in the brain. Animals were tested in Skinner boxes where they could stimulate themselves by pressing a lever. They received no other reward than the electrical stimulus in the course of the experiments. The primary findings may be listed as follows: (*a*) There are numerous places in the lower centers of the brain where electrical stimulation is rewarding in the sense that the experimental animal will stimulate itself in these places frequently and regularly for long periods of time if permitted to do so. (*b*) It is possible to obtain these results from as far back as the tegmentum, and as far forward as the septal area; from as far down as the subthalamus, and as far up as the cingulate gyrus of the cortex. (*c*) There are also sites in the lower centers where the effect is just the opposite: animals do everything possible to avoid stimulation. And there are neutral sites: animals do nothing to obtain or to avoid stimulation. (*d*) The reward results are obtained more dependably with electrode placements in some areas than others, the septal area being the most dependable to date. (*e*) In septal area preparations, the control exercised over the animal's behavior by means of this reward is extreme, possibly exceeding that exercised by any other reward previously used in animal experimentation.

The possibility that the reward results depended on some chronic painful consequences of the implantation operation was ruled out on the evidence that no physiological or behavioral signs of such pain could be found. The phenomenon was discussed as possibly laying a methodological foundation for a physiological study of the mechanisms of reward.

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Received July 15, 1954.

FAILURE TO FIND A LEARNED DRIVE BASED ON HUNGER; EVIDENCE FOR LEARNING MOTIVATED BY "EXPLORATION"[1]

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This paper reports two experiments. The first attempts to show that hungry rats rewarded by food will acquire a learned drive. The second explains certain paradoxical results of the first by showing that animals satiated on food and water will learn a new habit in order, apparently, to get the chance to explore and/or exercise.

Miller (11, 12) has presented a paradigm for showing that previously neutral stimuli have acquired learned drive value by demonstrating that they will motivate the learning of a new habit. An experiment on fear (11) used relatively massed trials in an apparatus consisting of a black and a white compartment separated by a sliding door. Rats were motivated by a shock in the white compartment to run through the door, which opened in front of them, and were rewarded by escaping the shock as soon as they entered the black compartment. After they had learned, they were given trials without the primary drive of pain from electric shock. During these trials without primary drive, they learned two new habits (first to rotate a wheel and then to press a bar) in order to escape from the white compartment. Before any training, they had shown no definite preference for the black compartment; control animals that had received similar training with a much weaker electric shock did not learn (12, p. 448). Therefore, it was concluded (*a*) that the white compartment was a neutral cue before its association with strong shock, and (*b*) that the learned drive (presumably fear) could motivate the acquisition of a new habit in exactly the same way as could hunger or any other primary drive.

In an additional experiment, Miller (10) compared a learned drive based on hunger with one based on electric shock. A new group of fear rats was trained in the way that has just been described; the other group was trained under 22-hr. hunger (superimposed on a restricted diet) to run from the white compartment to secure food in the black one, and then, after hunger had been satiated, was tested for new learning—pressing a bar to open the door. In this experiment, which used relatively massed trials, the fear animals learned to press the bar but the hunger ones did not. The failure of the hunger animals to learn in the test trials of this experiment serves as an additional control for factors such as innate preference for the black compartment or exploratory drive. But E. E. Anderson's (1) study of the "externalization of drive" suggests that a learned drive, initially based on hunger and rewarded by food, may be used to motivate new learning in satiated animals. The fact that Anderson used distributed trials (one a day), might account for the difference between his results and Miller's.

A study by Calvin, Bicknell, and Sperling (5) presents a different type of evidence which is interpreted as showing a learned drive based on hunger. The different measure used in this study is the amount of food eaten by moderately hungry animals in the presence of a stimulus that had been associated either with stronger hunger or with satiation. This study also used distributed trials.

EXPERIMENT I

The purpose of this experiment was (*a*) to repeat, with trials distributed one per day, Miller's attempt to use hunger to establish a learned drive capable of motivating satiated animals to learn a new habit, (*b*) to see if Anderson's (1) general procedure would produce learned drive in Miller's apparatus, and (*c*) to study the effect on the acquisition of the learned drive of different numbers of training trials motivated by the primary drive of hunger and rewarded by food.

Method

Subjects. The *S*s were 36 naive male albino rats of the Sprague-Dawley strain, 70 to 90 days old at the start of the experiment. They were housed in individual cages throughout the experiment.

Apparatus. The animals were run in Miller's learned drive apparatus, the essential features of which have

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[1] This investigation was supported by a research grant, M647, from the National Institute of Mental Health, of the National Institutes of Health, Public Health Service. The main findings were presented at the April 1954 meeting of the Eastern Psychological Association at New York.

been illustrated elsewhere (6, 11, 12). This consists of an enclosure 9 in. high by 6 in. wide by 48 in. long which is divided by a guillotine door into two compartments each 24 in. long. One compartment is painted white and has a grid floor, while the other is black with a solid floor of black metal. The front wall of both compartments is glass, allowing E to observe S. Each compartment contains a small socket hole in the rear wall about 4 in. above the floor and ¾ in. away from the guillotine door. A cylindrical brass rod ¼ in. in diameter may be inserted into either socket so that it protrudes 1 in. In Experiment I the bar was present at all times in the white compartment only.

The floor of the white compartment was hinged, so that when E placed S into it, a slight movement down closed a contact which started a Springfield timer. When it made the proper response (either touching the door or the bar, depending on how a switch was set), S completed a circuit to the grid floor so that a subthreshold current actuated a vacuum tube relay which stopped the timer and allowed the door to drop open.

A separate "activity box" apparatus was used to try to satiate any activity before test trials. It consisted of an open-topped rectangular enclosure 60 in. long by 30 in. wide by 24 in. high. Two additional walls bisected the length and width of this enclosure, dividing it into four identical compartments. To increase the opportunity for activity, the floor of each of these compartments was divided into four spaces by three parallel partitions 4 in. high.

Procedure. To insure a high level of hunger throughout drive-acquisition training, the animals were given only 1-hr. access to Purina Laboratory Checkers each day after water had been temporarily removed.

Taming was begun five days before the beginning of the experiment proper. Once a day, ½ hr. before the feeding time, each animal was picked up from its home cage and placed in another small cage which contained a small, 3-gm. pellet of wet ground Purina Chow. After eating the pellet, S was returned to the home cage.

Four groups, approximately equated for mean body weight, were randomly assigned to four experimental conditions: 70 trials, 30 trials, 10 trials, and 0 trials of drive-acquisition training.

The 70-trial group began training in the learned drive apparatus immediately, while the 30- and 10-trial groups were started 40 and 60 days later, respectively. Thus all three groups finished their training and were tested at the same time. Training trials were given one per day, so that drive-acquisition training required 70 days. In order that the taming, feeding, and handling experiences of animals in all four groups would be approximately the same, those groups *not* being run in the apparatus during these 70 days were removed from their home cages, fed a 3-gm. pellet of wet mash in another cage, and returned to the home cage once a day.

The drive-acquisition trials were run as follows: An animal was taken from its home cage and placed in the white compartment. In order to attach the response to as great a variety of orientational cues as possible, the animals were placed on odd-numbered trials at the far end of the compartment facing the closed door, and on even-numbered trials, in the middle of the compartment facing away from the door. When placed inside, S started the timer. When S touched the door, S stopped the timer, caused the door to drop open, and could enter the black compartment and eat the pellet which was on a small metal plate in the center of the floor. The rat was allowed to remain in the black compartment for 1 min. and then was gently lifted out and returned to the home cage. If it had not finished eating the pellet, S was allowed to carry it to the home cage. All animals learned to do this within four or five trials; before that E carried any uneaten portion to the rat's cage with S.

To facilitate learning and reduce initial fear, on the first trial the door was left open, and on the second trial the door was dropped as soon as the rat was within 8 in. of it.

The time for the animal to drop the door was recorded to the nearest .01 sec. for each trial. To normalize the distribution, the times were converted into speed scores by the formula $X = 100/t$. Since the animals were started from different orientations in the compartment on odd and even trials, scores were averaged over blocks of two trials.

After the 70-day drive-acquisition training, all animals were placed on an ad lib. diet of water and Purina Laboratory Checkers for the remainder of the experiment. They were allowed two weeks to recover from any effects of deprivation or "satiation shock." Then the second phase of the experiment, the test for learned drive, commenced.

All traces of food were removed from the apparatus. To insure complete satiation during these trials, each animal was given a supply of wet mash for 48 min. before its daily run in the apparatus. To minimize any exercise or activity drive during the test, each animal was placed, before its daily trial, in the activity box, where it could run and climb over the low partitions and eat bits of wet mash which were scattered about the floor.

Each animal went through the following routine: 28 min. with wet mash in the home cage; 16 min. with wet mash in the activity box; 4 min. more with wet mash in the home cage; then a test trial in the apparatus. In the extremely rare event that an animal was still eating when it was time for E to pick S up for a trial, S was given enough time to finish eating.

During the test trials, animals were always placed in the far end of the apparatus facing the door. The control of dropping the door was transferred from touching the door to touching the bar, which had always been present. There was no food in the apparatus. In order to cope with unusually long trials and eventual extinction, animals that had not touched the bar within 2 min. on any trial were removed to the detention cage. Animals that did press the bar were given a maximum of 1 min. in which to cross into the black compartment with all four feet so that the door could be closed by sliding it up. If an animal failed to enter within 1 min., it was removed to the detention cage. If it entered the black compartment, S remained there for 30 sec. and then was removed to the detention cage. After being in the detention cage for 8 min., all animals were returned to the home cage. The detention cage was used as a precaution against any reward effect of an immediate return to the home cage after removal from the black compartment.

All four groups were given 30 daily trials on the

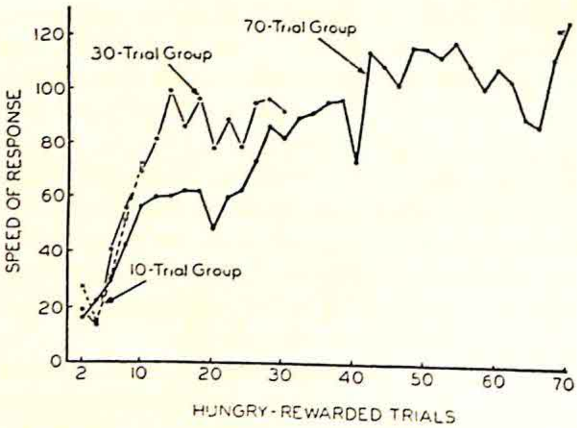

FIG. 1. Learning of the door-touching response by groups given various numbers of trials in the drive-acquisition apparatus. Speed of response = 100/time in sec. Trials plotted by pairs. The 30- and 10-trial groups had respectively 40 and 60 more days than the 70-trial group of preliminary handling and feeding while on the deprivation schedule.

new task of pressing the bar. The latency of bar pressing was recorded and transformed into a speed score.

Results

Figure 1 shows the learning of the door-touching response. All three groups learned readily. The 30- and 10-trial groups seemed to learn somewhat more rapidly than the 70-trial group, the 30-trial group being significantly superior for the sum of the first 30 trials ($p = .02$). The additional taming, handling, and feeding which the 10- and 30-trial groups had received before the beginning of training may have reduced their initial fear below that of the 70-trial group or may have given the food pellet additional secondary reward value.

Figure 2 shows how all four groups learn the new response of touching the bar when tested during the second phase of the experiment without the primary drive of hunger. All four groups show a definite learning curve; there are no reliable differences among them. Each animal's scores were summed for the first ten, middle ten, and last ten trials, and the resulting matrix of 108 scores for the 36 animals was used in an analysis of variance. The variance due to blocks of trials (learning) was highly significant ($p < .01$), while the differences among groups and the groups × trials interaction did not even approach significance. Thus it is clear that all groups learned, but there were no significant differences either in mean performance or in learning rate among the experimental groups. A further analysis of the blocks of trials variable shows that the differences between the first and second block and between the first and third block are highly significant ($p < .01$). Though there is a slight downward trend from the second to the third block, it is not significant ($p = .68$).

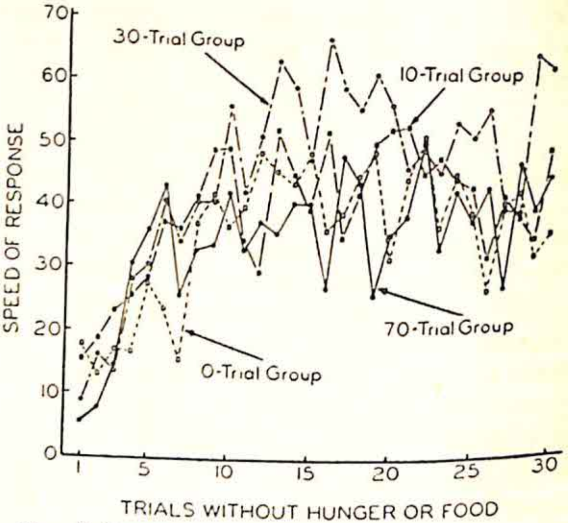

FIG. 2. Learning of the new bar-pressing response during trials without hunger drive and food reward by groups which had previously had various numbers of hungry and rewarded trials in the apparatus. Speed of response = 100/time in sec.

Finally, it should be noted that even the small differences that do exist among the four groups are not systematically related to the number of trials during drive-acquisition training. In mean speed of bar pressing, the four groups rank as follows: 30-trial, 0-trial, 70-trial, and 10-trial.

Discussion

The rats in the present experiment learned, irrespective of whether or not they had received previous drive-acquisition training. Does this mean that the animals in Miller's (10, 11, 12) previous studies of fear (described in the introduction to this paper) would have learned without any fear-acquisition training? Two control groups were involved in those studies composed of rats which had been given drive-acquisition training with either hunger (10) or weak electric shock (12, p. 448), respectively. Since neither control group showed any subsequent learning, it was concluded that drive-acquisition training with strong electric shock (presumably arousing fear) was essential for learning under the conditions of those experiments.

But why did the control animals in those experiments fail to learn the new habit of bar pressing while the animals in the present experiment did learn it? It is conceivable that the weak shock induced crouching or some other habit incompatible with subsequent learning, and that those animals would have learned if they had been run without any previous shock. In that case Miller's previous experiments would not be a valid demonstration of motivation by fear and reward by reduction in fear. It is difficult to imagine, however, why a *weak* shock should produce *more* interference with learning than the strong shock which did lead to subsequent learning. Furthermore, the control animals given drive-acquisition training with hunger failed to learn in the previous experiment but did learn in the present one. This suggests that the different results must have been produced by the one consistent difference in procedure, namely the spacing of the trials. In the previous experiment the trials were relatively massed, at 3-min. intervals, while in the present one they were widely distributed, one a day. It would seem that during spaced trials in our apparatus rats will learn without previous drive-acquisition training, but that during massed trials they will not learn unless they are motivated by some reasonably strong drive, such as fear established by painful electric shocks.

Since this assumption about the effects of massing the trials is so crucial to the interpretation of the previous experiments on fear, it will be tested further in the second experiment in this paper.

The rats in the 70-trial group in our experiment showed definite learning comparable to that of the rats in Anderson's (1) experimental group which was also run with trials spaced one a day. But this learning could not be attributed to *learned* drive in our experiment since the rats with no trials of drive acquisition learned equally well. Anderson's control rats also showed some learning. Since he does not present any tests of statistical reliability, it is possible that the fairly impressive difference between the means of his experimental and control groups was due to chance. It is also possible that the difference was reliable but was an artifact of interfering factors, such as fear of the maze and handling, which may not have been eliminated as completely for his control animals as for his experimental ones. His control animals were habituated in a shorter maze than the one used for pretraining the experimental animals. Furthermore, the feeding which was associated with the handling of the experimental animals may have helped to extinguish their interfering fears. In other words, the function of this feeding may have been not to externalize drive, but to reduce conflict. On the other hand, it is possible that the more complex task which Anderson used provided conditions which were more favorable either for acquiring learned drive or for measuring it. While our results do not disprove Anderson's conclusions, they cast some doubt on them and set a limit to the generality of their application.

Similar questions arise about the purported demonstration of learned hunger by Calvin *et al.* (5). Their conditions may have been more favorable than ours either because (*a*) eating may be a more sensitive measure than learning, (*b*) conditioning a drive may require the association of an *increase* in drive intensity with the to-be-conditioned stimuli (a state of affairs more probable in their experiment than ours), or (*c*) the close association with drive reduction in the black compartment of our apparatus may have produced an anticipatory relaxation which neutralized any learned drive in the white compartment (12, p. 451). Or possibly the difference between the two groups in their experiment came from a nausea conditioned to the cues during their association with satiation in the control group rather than from appetite conditioned to the cues during their association with hunger in the experimental group.

The most striking result of our experiment was the rapid learning of the new habit of bar pressing by the satiated and apparently nonrewarded animals irrespective of whether or not they had previous drive-acquisition training. Why do these animals, especially those in the 0-trial group, learn to press the bar? It seems possible that explanations could be developed in terms of light avoidance, exploratory drive, activity drive, curiosity, or Guthrie's (7) concept of stimulus change as a protection from retroactive inhibition. Conceivably the more conventional sources of primary or learned reward operated in some subtle fashion, but such factors had supposedly been reduced to a minimum both by satiating the animals and by delaying the handling and return to the home cage for some time after the bar was pressed. In an attempt to test some of these hypotheses, a second experiment was performed.

EXPERIMENT II

The purpose of the second experiment was to determine some of the conditions that are necessary for the learning which was observed in the first experiment. In order to test the hypothesis that the extensive handling, taming, and feeding of the 0-trial group was responsible for their learning, all rats were given briefer taming while satiated and without any food reward. To test the hypothesis of preference for the black compartment (e.g., from light avoidance), the first group was run from white to black while the second one was run in the *opposite* direction. This symmetrical type of a control for obvious, or even latent, preference is believed to be a particularly important one for experiments purporting to demonstrate learning from a motivation such as exploratory behavior, curiosity, or activity drive. To determine whether the sight and sound of the door dropping is sufficient to produce learning or whether entering and inspecting the black compartment is necessary, a third group was run from the white compartment but with a white panel fastened securely in place just behind the door. To determine whether spaced practice was necessary, a fourth group was run with massed trials. So that the massing would be comparable to that used in Miller's (10, 11) experiments on fear, it was necessary to eliminate the 16 min. in the activity box and 8 min. in the detention cage. In order to control for these changes in procedure, a fifth group was run with spaced trials, but with the periods in the activity box and detention cage omitted.

Method

Subjects. The *S*s were 50 naive male albino rats of the Sprague-Dawley strain, approximately 70 days old at the start of the experiment. All animals were maintained in individual cages on an ad lib. diet of water and Purina Laboratory Checkers.

Apparatus. The apparatus was identical with that used in Experiment I except for minor changes. For the animals running from the black compartment, pressure on its floor started the timer; touching a bar located in the same relative position as the one in the white compartment dropped the door and stopped the timer. In other words, the operations of running from white to black or black to white were similar.

Procedure. The animals were tamed by being handled once a day for five days when satiated *without* receiving any food reward. The first phase of Experiment I, hungry-reward training in the apparatus, was omitted. The animals were on ad lib. feeding throughout the experiment, and were fed wet mash for 48 min. before each training trial. Immediately after taming, the animals were divided into five groups of ten each, approximately equated for mean body weight, and randomly assigned to the following five experimental conditions:

1. *A white-to-black group* with a procedure duplicating that used in the second phase of the first experiment.
2. *A black-to-white group* run in exactly the same way but in the opposite direction. This was the only group started in the black compartment.
3. *A white panel group* run exactly like the first group except that when the door dropped, the animals were prevented from seeing or entering the black compartment by a white wooden panel immediately behind the door. To equate the effect of the time interval between bar pressing and being picked up and placed in the detention cage, each member of this group was given a partner in the white-to-black group and was removed from the apparatus at the moment which would make *S*'s interval on that trial equal to that of its just-previously-run partner.
4. *The massed group* received all 18 of their trials in a single afternoon with an intertrial interval averaging approximately 3 min. The ten animals in this group were randomly subdivided into three, four, and three animals, respectively, which were run on the first, middle, and last days of the experiment. To achieve the close massing, the activity box and detention cage were omitted from the procedure; the animals were returned immediately to their home cages (from which food and water had been temporarily removed) after each trial. In other respects, the procedure for the massed group was the same as that for the white-to-black group.
5. *The massed control group* was run without the activity box or detention cage to determine the effect of omitting these procedures. They were run exactly like the massed group except that their trials were distributed at the rate of one per day like those of the first three groups.

Results

All the latency scores were transformed into speed scores as described for Experiment I. The results are presented in Figure 3. The five groups start out at roughly the same level of performance; although the white panel and massed groups show little change through-

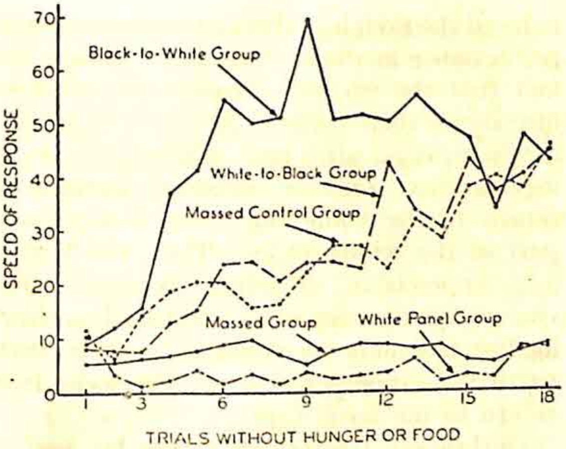

FIG. 3. Effect of experimental conditions on learning of the bar-pressing response by groups trained without hunger drive or food reward. Speed of response = 100/time in sec.

out the 18 trials, the others show definite learning.

Each animal's scores were summed for the first six, middle six, and last six trials, and the resulting matrix of 150 scores for the 50 animals was subjected to analysis of variance to assess the over-all effects due to blocks of trials, groups, and groups × trials interaction. All three produced highly significant F's, with p in each case less than .01. Table 1 summarizes this analysis.

Then, for the mean of all 18 trials, separate t tests were computed comparing each group with every other one. Of these ten comparisons, all but two produced differences significant at the .01 level of confidence or beyond. The difference between the white-to-black and massed control groups and between the massed and white panel groups were not significant ($p = .79$ and .59, respectively).

Next, the significance of the *trend* for each group was analyzed by computing separate t tests among the three blocks of six trials. None of the comparisons among blocks of trials even approached significance for either the massed or white panel groups. The other three groups all showed an increase from the first to the third block of trials significant beyond the .01 level of confidence. These three groups also showed significant increases from the first to the second block, and from the second to the third block, with the exception of the black-to-white group, which showed a significant *decrement* from the second to the third block of trials.

TABLE 1

Analysis of Variance of Speed Scores in Experiment II

Source of Variance	Mean Square	df	F	p
1. Groups..........	2,716,275*	4	13.86	<.01
2. Trials...........	865,061**	2	71.48	<.01
3. Trials × Groups...	221,908**	8	18.34	<.01
4. Rats within groups.	196,031	45		
5. Rats within groups × Trials.......	12,102	90		

* Tested against 4.

** Tested against 5.

Since all groups started from nearly the same level of performance, the foregoing analysis gives a fairly complete picture of the differences among the five groups. As a further check, separate t tests were computed on the differences between trends among the five groups. An examination of the resulting 30 comparisons simply confirms the impression one gets from an examination of Figure 3. There is little difference between the white-to-black and massed control groups or between the massed and white panel groups at any stage of training.

After pressing the bar, all the animals (except those prevented by the white panel) at least poked their heads into the other compartment and sniffed around. More of the animals going to the white entered all the way than of those going to the black. On the first trial, the difference between the black-to-white group and each of the others was significant beyond the .01 level.

For the first 18 trials during which a direct comparison is possible, there is little or no difference between the learning by the white-to-black group in Experiment II and by the 70-trial group (white-to-black) in Experiment I. Though the rats that had had 70 drive-acquisition trials before the test may show some slight superiority in early trials (presumably because their fear of the door's dropping has been extinguished), the mean speed for these animals averaged over all 18 trials is not significantly greater than that for the white-to-black group of Experiment II ($p = .38$).

Discussion

The main results of Experiment II were as follows: (*a*) Satiated and nonrewarded animals will learn the bar-pressing response either to open the door from the white to the black compartment or from the black to the white compartment. (*b*) Animals that pressed the bar (in the white compartment) to drop the door but were prevented from seeing or entering the other compartment did not learn. (*c*) Animals trained with massed instead of spaced trials (white-to-black) did not learn. (*d*) The failure of the massed group to learn was not due to the omission of the activity box and detention cage from their running procedure because the massed control group, which was given spaced trials with these procedures omitted, learned as well as the white-to-black group.

The fact that the black-to-white group learned faster than the white-to-black group suggests that a preference for the white compartment may be a source of some motivation and reward in the apparatus. However, the fact that both groups (running in opposite directions) learned shows that such a preference is not a necessary condition for learning. Apparently the fact that pressing the bar is followed by the chance to observe and enter a new compartment is sufficient to produce learning.

The fact that the white panel group did not learn shows that the cues produced by bar pressing and door dropping, or by being picked up and returned to the home cage via the detention cage, are not sufficient to produce learning; it suggests that the act of seeing or exploring the other compartment, or perhaps experiencing the change between the two compartments (irrespective of the direction of change), produces the reinforcement. But we cannot tell whether or not exposure to the new stimuli in the other compartment would produce learning even if the animals were prevented from entering or exploring.

Since dropping the door provided the animals with more space in which to move about, it might be argued that the reinforcement came from this greater opportunity to exercise or escape restriction. However, the white-to-black group did not seem to perform any worse than the massed control group which was run under identical conditions except for the omission of the activity box and detention cage. Presumably exercise in the activity box before each trial, as opposed to confinement in the small home cage, would have reduced the exercise drive and produced poorer performance in the white-to-black group. The fact that the massed controls were returned directly to their home cage, rather than to a detention cage, after each trial might also be expected to produce superior learning if return to the home cage were a significant part of the reinforcement. Thus, the lack of any appreciable difference between these two groups also serves as additional evidence against assigning an important role in these particular experiments to reinforcement from return to the home cage.

Guthrie's (7) principles might be used to explain the learning shown by groups that had a chance to enter the other compartment and were run with distributed practice. Pressing the bar would be the last thing that the animal did before entering the other compartment, where the change in cues would protect *S* from unlearning the habit of pressing the bar by removing the opportunity to perform different responses to the original cues. But this explanation—at least in its simplest, most obvious form—would seem to apply equally well to the massed group which did *not* learn. If it is assumed that general changes in posture and other sources of interoceptive stimulation are more likely to occur during the longer interval, the task of the animals with distributed practice would be more difficult, since they would have to attach the response of pressing the bar to a greater variety of combinations of cues. Thus it seems that a simple form of Guthrie-type explanation is not able to account for the difference between the learning of the groups with massed and distributed practice.

The failure of the massed group to learn confirms the conclusion from Miller's (10, 11, 12) previous studies that learning will not occur during *massed trials* in his apparatus unless specific procedures have been used to establish a learned drive, such as fear.

Though some inferiority of the massed group would be expected from the principle of reactive inhibition (9), the magnitude of the difference found in this experiment suggests that other factors may be operating. If learning were motivated by a relatively weak drive of exercise, exploration, or curiosity, it is possible that this motivation might be satiated or extinguished by the massed practice and not have enough chance to recover during the short time between trials. Montgomery (14, 15, 16) and Berlyne (2) have shown that a rat's tendency to investigate a new stimulus object decreases rapidly with continued exposure and shows little recovery during a short interval of nonexposure but considerable recovery during a 24-hr. interval. Thus, the satiation of an exploratory drive during massed trials but recovery during spaced ones may account for the difference in the second experiment. If an exploratory tendency can produce learning like other drives such as hunger, and also show a similar pattern of satiation and recovery, these functional parallels to already known drives would help to justify its classification in the same category with them, namely as a drive.[2]

A considerable body of challenging experimental work interpreted in terms of "exploratory" and "manipulatory" drives has been reported by Harlow and his associates (8). Harlow believes that these drives differ from the better-studied ones, such as hunger, in that external stimuli, i.e., the ones explored, both elicit the drive and operate as reinforcement.

We, however, would not put a drive in a special category simply because it is elicited by external stimuli. We prefer the drive-reduction hypothesis developed by Hull (9) and Miller and Dollard (13), which treats externally elicited drives (such as pain) in the same way as other drives. Furthermore, as Brown (4) has pointed out, in some of the Wisconsin studies on the "visual exploration drive" the novel stimuli to be explored are not present at the time the animal begins working to secure them. If the novel stimuli elicit the drive, this would mean that the drive is produced *after* the animal has performed the response the drive is supposed to be motivating.

If, as Harlow seems to imply, the same novel stimuli elicit an exploratory drive and *simultaneously* serve as an exploratory reward, a strict drive-reduction theory would be unable to deal with these phenomena. However, we believe it is possible that confinement produces anxiety, restraint is frustrating, or monotony arouses a drive of boredom. Indeed, the observation of small children who are required to sit absolutely still, the reports of prisoners subjected to solitary confinement, and the difficulty of Bexton, Heron, and Scott (3) in retaining *S*s in their experiment on the effects of decreased sensory variation would indicate that such conditions can produce strong motivation. Therefore, we suggest that drives produced by homogeneous or monotonous stimulation, enforced inaction, etc., may be reduced by sensory variety, freedom of action, etc., and that such drive reduction is the *reinforcement* involved in learning for "exploratory," "manipulatory," and "exercise" rewards. For the present, we choose the more parsimonious alternative of trying to analyze such concepts as exploratory drive along the same lines as conventional drives.

We also believe some writers have been too quick to assume that novel stimuli elicit a drive simply because such stimuli commonly elicit activity or exploration. This may well be a case of confusing the cue properties of a stimulus with possible drive properties. Exploration may be an innate response to novelty in some species, or it may occur because exploration has been reinforced in the presence of novel cues in the animal's past history. Activity is a poor measure of drive; some drives, such as fatigue or fear, may tend to decrease activity.

Irrespective of how the foregoing problems of theory and interpretation are handled, we agree that it is extremely important to develop techniques for studying significant sources of motivation which have previously been neglected. Such studies may lead to fundamental extensions or radical revisions of our present concepts. Certainly our present list of experimentally studied motives is far too short.

SUMMARY

Experiment I. Four groups of hungry rats were given 70, 30, 10, and 0 drive-acquisition trials in Miller's learned-drive apparatus with food reward in the goal compartment. The animals were started in the white compartment and learned to touch the door to open it and run into the black compartment containing the food. In a subsequent test for learned drive, these four groups, now satiated and nonrewarded, were required to learn the new response of pressing a bar to open the door to the goal compartment.

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[2] According to observations by Sharpless (17), novel stimuli elicit an "arousal reaction" presumably involving the brain-stem reticular formation. This "arousal reaction," indicated by characteristic changes in brain waves, shows fairly rapid extinction (presumably as the stimulous loses its novelty) and eventual recovery analogous to that described above. It is conceivable that this arousal reaction to novel stimuli is part of the mechanism of exploratory motivation.

All four groups learned to press the bar, but there were no significant differences among the four drive-acquisition groups. The experiment (*a*) does not provide any evidence for a learned drive based on hunger and food reward, and (*b*) shows that rats with no prior experience in the apparatus will learn to press the bar while satiated and without the reward of food.

There is a brief discussion of possible artifacts in previous experiments purporting to show a learned drive based on hunger.

Experiment II. Rats satiated for food and water were trained in the learned-drive apparatus to press the bar in one compartment to gain access, through the door, to the other compartment. No food or water reward was present in the apparatus at any time.

It was found that: (*a*) Animals will learn to press the bar either to gain entry to the black compartment from the white one, or vice versa. (*b*) Animals that responded in the white compartment but were not allowed to see or enter the black compartment did not learn. (*c*) Animals trained (in the white-to-black situation) with massed instead of spaced trials did not learn.

A simple application of Guthrie's concept of stimulus change as a basis for a persisting habit does not seem to be able to explain the marked difference between the groups with massed and distributed practice. Explanations in terms of exploratory or activity drive are discussed.

The absence of learning during massed trials in these experiments confirms the results of two control groups used in Miller's previous experiments on fear and shows that the learning which he observed during massed trials following strong electric shocks would not have occurred without these shocks, which presumably established a strong learned drive of fear.

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Received February 24, 1954.

QUANTIFICATION AND COMPARISON OF SEX DRIVES UNDER VARIOUS CONDITIONS IN TERMS OF A LEARNED RESPONSE[1]

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The problem of this study is to find and use a more sensitive measure of the sex drive than the sex responses.

The natural or "consummatory" responses associated with sex drive such as fore play, intromission, and male ejaculation are very difficult to compare quantitatively. Each sex response series varies from every other in terms of the relative numbers and durations of the various components. It seems doubtful, furthermore, that any one ejaculation is quantitatively equivalent to any other ejaculation, either within or between individuals. Nevertheless, such responses have been widely used by students of sexual behavior (1, 2, 3, 4, 5, 10). As Soulairac (6) writes, ejaculation and intromission may even have different endocrine backgrounds. It is, then, hard to know how to weight these various elements, to compare and combine them, etc. Stone, Tomilin, and Barker (7) used the Columbia obstruction apparatus to measure drive strength. The introduction of strong noxious stimuli into a situation already replete with unknown variables probably should be avoided. The interjection of another drive—hunger—whose physiological, sensory, and proprioceptive bases are no better understood than those of sexual drives (cf. Stone and Ferguson, 8), certainly further complicates an already complex situation. Veneziano (9) obtained data indicating the possibility of a rat's learning a multiple T maze under sex drive.

A learned response that is to be used in measuring a drive should itself be as free from drive-producing or decreasing components as possible. It should, therefore, be easy for the animal to learn and nonfatiguing to perform. The response of turning a small wheel was felt to meet these requirements.

METHOD

Twenty-two adult male albino rats of the Sprague-Dawley strain were subjected to the following training and testing schedule:

Test for copulatory performance. All animals used met the criterion of three successive successful tests at five-day intervals. A successful test was one in which the male ejaculated within the 20-min. test period.

Cage conditioning. All *S*s were placed individually in the experimental cage for 10 min. on each of two days. This cage measured approximately 18 by 18 by 12 in. It had a small wheel available at one corner, and a holding cage with a sliding floor flush with the ceiling of the larger cage in another corner. The wheel was immovable when the experiment was not in progress.

Training and testing. For his first experimental run the male was placed gently in the testing cage with the wheel locked, and a stop watch was started. After 2 min. the wheel was unlocked and given a turn by *E*. As soon as the male turned the wheel one revolution, the time was noted and a receptive female was dropped through the trap door to him. The latency from the availability of the female to the first copulation was recorded. After five copulations the time was noted, and the female was replaced in the holding cage. The interval until the male once again turned the wheel was recorded and the female again dropped through the door. This procedure was repeated until the male achieved an ejaculation or until the 20 min. had elapsed. If an ejaculation occurred, the female was immediately placed in the holding cage. The interval from this time until the male turned the wheel was known as the absolute postejaculatory latency, and that ensuing between this wheel turning and the first postejaculatory copulation, the relative postejaculatory latency. Periods of five copulations were allowed and timed as before until the test period terminated. Six training-testing periods of 20 min. each were given at weekly intervals to all animals.

Extinction trials. Following the series of six training-testing trials, extinction trials began. These were identical to the preceding trials except that the receptive female was not dropped to the male, and the duration of each period was 10 min., to give more distributed trials. The number of revolutions given the wheel in each minute was recorded.

RESULTS

Wheel-Turning Performance

Secondary-cue initial latency. This was the time from the turning of the wheel by *E* until the animal turned the wheel. The averages for the six trials ranged from 19.1 to 262.5 sec.

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[1] This study was conducted while the author was the guest of Frank A. Beach and the psychology department of Yale University, under the terms of a Ford Foundation Fund for the Advancement of Education grant.

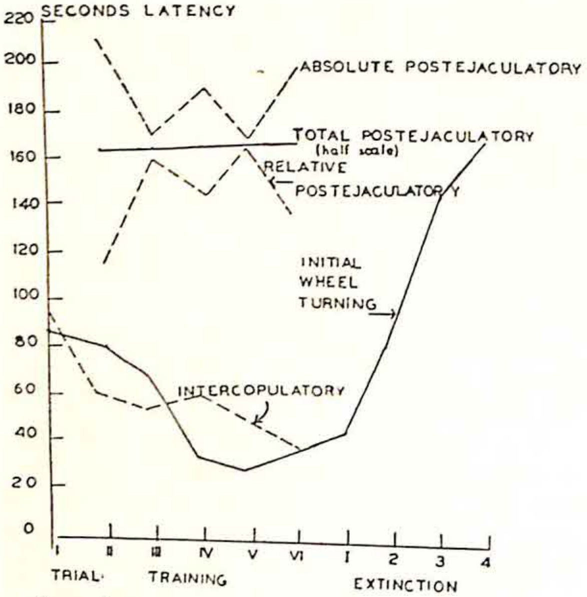

FIG. 1. Average wheel-turning and sexual performance latencies

with a mean average of 64.05 sec. The averages for the 22 animals on each trial showed an irregular drop from 99.54 sec. on the first trial to 43.63 sec. on the last trial. During extinction trials the average rose from 30.7 sec. on the first trial to 170.0 sec. on the last.

Intercopulatory latencies. These were periods from the removal of the female following a given five copulations until the male once again turned the wheel. The precopulatory latency was the time from the first presentation of the female to the first copulation. This latency averaged 83.0 sec. for all trials. This was not, of course, a wheel-turning latency.

The first intercopulatory latency was that between copulations 5 and 6. It averaged 75.9 sec. for all trials. It showed a fairly consistent drop, from 130 to 38 sec. during the learning trials.

The second intercopulatory latency was that between copulations 10 and 11. It averaged 60 sec. for all trials and showed a drop from 106.4 to 42.9 sec.

The postejaculatory latency was divided into two subperiods: the absolute period, from the removal of the female after the ejaculation until the male turned the wheel again, and the relative latency, from the time the female entered the experimental cage as the result of this wheel turning to the first postejaculatory copulation. Only the absolute postejaculatory period represents a wheel-turning latency. It averaged 188 sec. and showed no regular trend during the course of the trials. The relative postejaculatory latency likewise showed no regular trend and averaged 145.7 sec. The total postejaculatory latency remained markedly constant for those showing postejaculatory activity (see Fig. 1).

Wheel-turning extinction. The average number of wheel revolutions per animal fell from 39.3 on the first extinction trial to 12.8 on the fourth. Five of the 22 animals had stopped turning the wheel entirely by this time.

Reproductive Performance

Ejaculation. Although all experimental animals had reached the criterion of three successive ejaculations, five failed to ejaculate during the training and testing period. One showed 16 per cent ejaculation; five reached 50 per cent; two gave 67 per cent results; three were 84 per cent effective; and six ejaculated at all opportunities.

Time for ejaculation. The experimental animals required an average of 12.19 min. from the time they were first presented with the receptive female to reach ejaculation. The range was from 4.5 to 19.7 min. These times included the intercopulatory latencies.

Copulations to first ejaculation. The rats copulated between 8 and 20 times, on the average, before reaching ejaculation. The mean number of copulations before the first plug was delivered was 13.8. Those rats requiring the fewest copulations to reach climax were most likely to ejaculate on every opportunity ($\rho = .48 \pm .181$, significant at the .05 level).

Copulation rate. This datum is derived from the number of copulations before the first ejaculation divided by the active copulation time preceding this end point. It ranged from 1 copulation per 19.2 sec. to 1 per 73.3 sec. The over-all average was 1 in 39 sec. There seems to be little correlation between copulation rate and probability of ejaculation.

DISCUSSION

Great variation was apparent in and between the individuals' performance of the recently learned response of wheel turning and the more natural responses associated with sex drive. An animal might turn the wheel rapidly and frequently and have little to do with the receptive female; the converse was equally true. Therefore, it was felt that rank-order correlation coefficients [$\rho = 6\Sigma(D^2)/N(N^2 - 1)$] between wheel-turning latencies and the "natural" expressions of sex drive might be indicative. In each case the rank order of wheel-turning latencies is compared with that of the listed criterion:

Sex Response	ρ
Copulations to the first ejaculation	.01
Time to the first ejaculation	.17
Copulation rate	−.05
Probability of ejaculation	.02
Relative postejaculatory latency	−.30

The only thing that wheel-turning latency correlated with was the number of turns during extinction trials, .51 ± .174. In other words, the quicker an animal tended to turn the wheel, the longer it took him to extinguish when the response was no longer reinforced. This is, however, in a sense, simply comparing one aspect of wheel turning with another and indicates nothing as to a common drive factor with sex responses.

The number of turns made during extinction trials might be indicative of the drive active at the time, which in turn might be related to the quantity of drive active during the reinforced trials. As a check on this possibility, rank-order coefficients between the number of extinction turns and the various sex responses were determined:

Sex Response	ρ
Copulations to the first ejaculation	.23
Reciprocal of time to the first ejaculation	.45 ± .187
Copulation rate	.29
Probability of ejaculation	.31
Relative postejaculatory latency	.63 ± .142

The last of these coefficients would seem to deserve special attention. It means that animals that tend to give the most turns during extinction—require the greatest ${}_sI_R$ to negate the ${}_sE_R$ in Hullian terms—are those that take longest to recover from ejaculation. Could it be that in them the drive is more adequately reduced, leading to the necessity of a longer recovery period before they will again copulate, and at the same time that they have a stronger ${}_sH_R$ established, requiring more unreinforced responses to extinguish?

It is noticeable that extinction turns seem to correlate better, on the average, with all the more natural sex responses than do the wheel-turning latencies, the average of coefficients for extinction turns being .38, compared with an average of coefficients for wheel-turning latencies of only .11, neglecting sign. It is possible that the device used in measuring sex drive was not as free from drive production as it might have been. Although the wheel was small, so that the rat turned it with forefeet only, it may have aroused exploratory drive. Another paper is now all but complete in which bar pressing was the response used to measure sex drive. This response should not be intrinsically drive-arousing or reducing, and the results, therefore, should be more clear cut.

SUMMARY

A first attempt to find a measure of sex drive in terms of an easily quantifiable response involved the determination of various latencies connected with turning a small wheel, and other latencies associated with the more natural or consummatory sex responses. Although little correlation appeared to exist between these two types of latency, a more significant correlation was found between number of wheel turns during extinction and previous consummatory sex responses. Investigation of possibilities suggested by this latter finding is being continued.

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Received February 22, 1954.

THE SECONDARY REWARD VALUE OF FOOD FOR SATIATED ANIMALS[1]

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After a review of latent learning studies Thistlethwaite (4) stated that irrelevant incentives do not function as learned rewards during the latent period. To test this proposition 8-hr. thirsty, food-satiated rats were trained to traverse a runway (6). Half the *S*s ran to an empty goal box, and the other half to an irrelevant incentive—food pellets scattered on the goal-box floor. Since the secondary reward group ran faster and more consistently, it was concluded that a learned reward *is* effective when another primary drive is active. This conclusion ignores the interaction of hunger and thirst; e.g., it is known that *S*s deprived of water reduce their food intake. Therefore, it is likely that a weak hunger drive was also operating.

The purpose of the present investigation is to determine whether or not a secondary reinforcing agent will facilitate runway performance when the primary drives of hunger and thirst are satiated. Two additional aspects of interest are to study the effects of two satiation techniques and to see if the secondary reinforcing agent will lose its potency after an extended period of tests.

EXPERIMENT I

Method

Subjects. The *S*s were 23 naive male Sprague-Dawley rats approximately 75 days of age. They were secured from the Sunset Hills Farm of Lawrence, Kansas. The *S*s were assigned at random to the two treatments described below. One *S* was discarded in pretraining because of excessive timidity, leaving two groups of 11 *S*s each.

Apparatus. The alley runway previously employed (6) was used. Elevation of the starting-box door activated a standard timer, which was stopped when the weight of *S*'s body depressed a floor panel at the goal-box entrance. The basic response measure, running time, was defined as the elapsed time between these two events.

Pretraining procedure. During the first five days *S*s were gentled, and a mash satiation regimen was instituted. At 8 A.M. the food pellets and water bottles were removed from the living cages. At 12:00 N. they were returned. Three hours later dishes of wet mash and water were placed in the cages for 1 hr. Since some *S*s drank after handling, the water dishes were left in the cages for an additional 15 min. prior to running. The individual handling cages in the experimental room were equipped with water bottles and dishes of food pellets.

On day 6, *S*s in squads of five or six explored the empty runway for 15 min. On days 7 and 8 each *S* underwent a single runway trial. The results of these trials disclosed that the means and variances of two independent groups differed only within the limits of sampling error.

Test procedure. In the subsequent 20-day test period *S*s received one trial per day. Food pellets were scattered on the goal-box floor for the experimental group, whereas the control *S*s ran to an empty end box. On day 21 half of the *S*s in each treatment were given ten massed trials, and on day 22 the remaining *S*s had ten massed trials. During all trials *S*s were confined in the goal box for 20 sec. before being returned to their individual handling cages. On the massed trials *S*s spent 30 sec. in the individual cages between trials. Throughout the test period the mash-satiation technique was utilized.

EXPERIMENT II

Method

Subjects. The *S*s were 23 naive 90-day-old Sprague-Dawley albino rats and were obtained from the same source as above. Eleven *S*s were assigned at random to an experimental group and the other 12 *S*s to the control group.

Pretraining procedure. The procedure was identical to that of Experiment I except that an ad libitum satiation method was employed. Food pellets and water were available in the home cages at all times with the exception of 30 min. following the completion of the daily procedures when the water bottles were absent. Thus the only difference between the maintenance schedule in this experiment and the earlier one (6) was that *S*s had unlimited access to both food and water. Because the groups performed differently on days 7 and 8, ten closely matched pairs of *S*s were selected, and the two rats in each pair were randomly assigned to the experimental and control group.

Test procedure. The test procedure was similar to that of Experiment I except that a single trial was administered daily for a 30-day period. Again, the control *S*s were run to an empty end box and the experimental *S*s to the irrelevant incentive, food pellets on the end-box floor. In this period a matched pair of *S*s was eliminated when an experimental *S* ate a pellet on the thirteenth trial.

RESULTS

The median running times for successive blocks of five trials in Experiment I are shown in Figure 1. The application of Wilcoxon's *T* test for unpaired replicates (7) revealed that the differences between the groups were significant at less than the .02 level on trials

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[1] This research was supported by the Faculty Research Committee, University of Kansas.

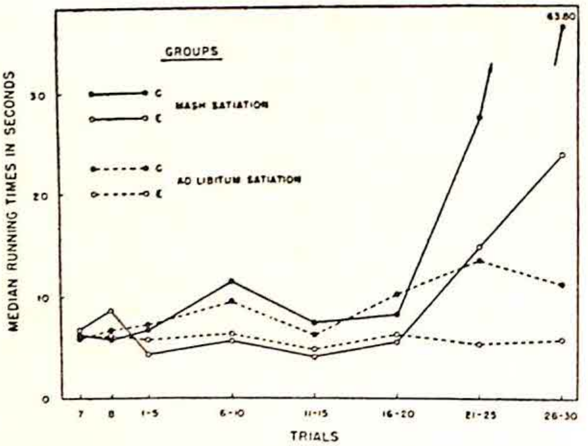

FIG. 1. Median running times in seconds during the two matching trials and the 30 test trials for the control and experimental groups in Experiments I and II

6 to 10, just above the .05 level on trials 11 to 15, and at the .02 level on trials 26 to 30. To secure an over-all statistical test of the effectiveness of the secondary reinforcement during the distributed trials the median of each *S*'s medians on the four blocks of trials was computed. A test between the groups yielded a *T* of 88, which was significant between the .01 and .02 levels of confidence. Although the groups had homogeneous variances in pretraining ($F = 1.65$, $p > .10$), the over-all median running times for the control *S*s appeared to be far more variable. Since the distributions of medians were badly skewed, they were normalized by a logarithmic transformation. The homogeneity of variance test on the transformed scores showed that the control group was more inconsistent ($F = 8.21$, $p < .01$). Finally, an examination of the separate trial medians showed that the learned reward group ran faster on 26 out of the 30 trials. All these comparisons lead to the conclusion that an irrelevant incentive possesses reward value when the primary drives of thirst and hunger are satiated.

The induction of satiation by the ad libitum method in Experiment II resulted in the same general performance trends observed in Experiment I (see Fig. 1). The small but consistent differences in the median running times in favor of the learned reward group were assessed by the signed rank test (7).[2] The difference between the groups was significant at the .02 level on trials 11 to 15, just above the .05 level on trials 16 to 20 ($T = 7$; $T_{.05} = 6$), and at less than the .05 level on trials 21 to 25. An over-all comparison, utilizing the median of each *S*'s medians for the six blocks of trials, was significant at the .02 level of confidence. A *t* test for correlated variances (5) showed the over-all medians of the experimental *S*s to be less variable ($t = 5.23$, $p < .005$). And again the experimental group's individual trial medians were smaller than those of the control group on 27 of the 30 trials.

The curves in Figure 1 suggest that the two satiation methods did not produce differential effects. To confirm this observation Festinger's *d* test (1) was applied to the secondary reinforcement groups from Experiment I and II on the first four blocks of trials and to the two control groups during the same periods. Because none of these eight comparisons approached significance, we may conclude that there was no difference in the performance of the animals that were subjected to the mash-satiation technique and those that experienced the ad libitum method.

The persistence of the learned reward through time is evident from Figure 1. In Experiment I the secondary reward *S*s continued running rapidly for 20 days. Even when the trials were massed on trials 21 to 30, the experimental group displayed a greater resistance to response disruption than that manifested by the controls. In Experiment II, where all the trials were spaced, the irrelevant incentive still appeared effective after 30 days of running.

Finally, the results of the present two experiments and of the earlier investigation (6) may be contrasted. In the three experiments the over-all median running times were significantly shorter for the secondary reward *S*s. Even more striking was the effect of the secondary incentive on the running time variability. The *S*s running to an empty end box exhibited far greater inconsistency in their performance. A third difference observed in the three experiments was for the experimental group's median response time to be shorter than the control group's on a high proportion of the individual trials. We may conclude that the secondary incentive is effective either when another primary drive is present or when the thirst and hunger drives are satiated.

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[2] This statistical test was applied because *S*s were matched in Experiment II.

DISCUSSION

Generally token rewards are subject to experimental extinction (2). Yet in the present set of experiments the learned reward still appears influential at the termination of testing. We contend that this persistence is due both to its long past history of association with drive reduction and to the fact that the reward value of the food is constantly being renewed when *S*s feed in their home cages. The recurrent coupling of the perceptual properties of food and hunger reduction in the living cages serves to forestall such extinction.

An alternative explanation for the persistence of the runway response under satiation conditions involves the postulation of a strong exploratory drive. When the "primary" drives of hunger and thirst are slaked, this drive becomes dominant (3). It is maintained at a high level, during the distributed trials, by the single exposure to the apparatus daily. The superiority of the experimental *S*s could then be attributed to the presence of food pellets as objects to be explored. The tenability of this hypothesis would have to be investigated by running control *S*s to inedible objects.

In retrospect the failure of the two satiation techniques to produce differential effects does not seem too surprising. The major difference between the two treatments was that the mash-satiated *S*s were deprived of food and water for a 4-hr. period each day while the ad libitum *S*s never experienced deprivation. It is possible that extended periods of deprivation would bring about more complete satiation and reduce the learned reward value of the irrelevant incentive.

Finally, it should be noted that the results of the present and previous (6) experiments are not in accord with Thistlethwaite's conclusion (4) that irrelevant incentives do not function as learned rewards during the latent period. Contrary to this position, we have found the secondary incentive to be effective either when another primary drive is present or when the primary drives of thirst and hunger are satiated.

SUMMARY

The primary purpose of these two investigations was to determine whether or not an irrelevant incentive, the sight of food, acts as a learned reward for *S*s satiated for food and water. Secondarily, the persistence of such acquired reward value and the effects of two techniques for inducing satiation were studied. Since the experimental *S*s, traversing a runway to an end box containing food, ran more rapidly and consistently than the control *S*s running to an empty goal box, it was concluded that the sight of food has reward value when the primary drives of hunger and thirst are satiated.

The learned reward value and its observed persistence were attributed to the historical and contemporary association of the learned reward with drive reduction. Another explanation for these phenomena involved positing an exploratory drive and conceiving of the food pellets as objects for exploration and manipulation. This hypothesis requires further experimentation to assess its truth value.

The two satiation techniques did not produce differences in performance in either the control or experimental groups. It was suggested that the 4-hr. deprivation followed by mash feeding and the ad libitum schedules were not sufficiently dissimilar to yield different behavioral outcomes.

Lastly, the discordance between the present results and Thistlethwaite's position was pointed out.

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Received July 2, 1954.
Early Publication.

CHANGES IN THE SELF-SELECTION PATTERN FOR PURIFIED DIETARY COMPONENTS BY RATS AFTER STARVATION[1, 2]

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Nutritionists have demonstrated that certain diets are more efficient than others for the rehabilitation of rats after starvation. There is also evidence that some diets fed to rats after starvation have harmful physiological effects. The present experiment was designed to test the ability of rats to self-select an optimum diet for rehabilitation and to obtain additional information on the changes in patterns of selection of purified dietary components after a period of starvation.

Experimental results differ with regard to which diets are more efficient for rehabilitation of rats after a period of starvation (2, 3, 10). In an experiment on rehabilitation after three types of dietary restriction, DaCosta and Clayton (2) found that, independently of the preceding dietary restriction, the rats rehabilitated with a high-fat diet gained weight more rapidly than those rehabilitated with other diets. A high-protein diet produced the slowest weight recovery, and a high-carbohydrate diet had an intermediate effect. However, Krehl and McNulty (3), in describing a similar experiment, state that they found no significant differences in weight gains of rats rehabilitated by a high-fat, high-protein, or high-carbohydrate diet after a starvation that produced 30 per cent reduction in weight. They also reported that adult rats placed on a self-selection diet after a starvation period fell into two groups: (*a*) those that regained weight at a reduced rate and (*b*) those completely unable to gain. After rehabilitation on the self-selected diet or on a prepared diet, the rats were starved a second time and placed on self-selection. This time all the rats made a more rapid recovery, and 100 per cent of those on self-selection for a second time selected adequately. There was no mention of how much of each component was eaten during rehabilitation. Winter (10) reported that the forced feeding of carbohydrates to rats after starvation produced lesions of the gut as well as other physiological disturbances.

Andik and associates (1) gave rats a free choice of a high-fat, a high-protein, or a high-carbohydrate diet after six days of starvation and found that the animals chose more of the high-fat diet than of either of the other two. Goetzl (11) has indicated that rats which were on a self-selected diet consisting of fat, carbohydrate, protein, and a salt mixture, and supplied with vitamins, will, after a two-day period of starvation, choose significantly more fat and significantly less protein and carbohydrate. Data from an experiment by Pilgrim and Patton (7), in which, incidental to the purpose of the experiment, rats on a self-selected diet were starved for a period of two days and subsequently put on self-selection again, did not show the same trend.

METHOD

Subjects and Apparatus

The *S*s, 43 male rats of the Sprague-Dawley strain, were received at 40 days of age, with a weight range of 125 to 150 gm. The animals were housed in individual cages with aluminum racks to hold the food cups in separate compartments. These racks, especially constructed to be used with a conical food cup to minimize spillage, permitted weighing the food that was spilled.

Procedure

From 40 to 49 days of age the rats were fed Purina Chow and water ad libitum. From 50 to 60 days of age the diet was changed to a mixed purified diet consisting of 25 per cent hydrogenated vegetable fat (Crisco), 25 per cent casein (Labco, "vitamin-free"), 45 per cent sucrose, and 5 per cent salts IV (5). They were given vitamins daily in two solutions, the water-soluble vitamins in 20 per cent alcohol, the oil-soluble vitamins in corn oil. The daily dosage, fed by dropper, was about

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[1] Part of this material was presented at the meetings of the American Psychological Association, September 1953, in Cleveland, Ohio.

[2] This paper reports research undertaken at the Quartermaster Food and Container Institute for the Armed Forces, and has been assigned No. 460 in the series of papers approved for publication. The views or conclusions contained in this report are those of the authors. They are not to be construed as necessarily reflecting the views or indorsement of the Department of Defense.

four times the known requirements.[3] In order to accustom the rats to eating from the cups in the rack, the mixed purified diet was randomly moved from one compartment to another during this phase of the experiment. To familiarize the rats with casein, which is known to be rejected by many rats placed on self-selection (6, 8), it also was presented in the same manner as the purified diet.

At 61 days of age (weight range 201 to 265 gm.) all 43 rats were placed on self-selection, the diet consisting of the four food components used in making the mixed purified diet, with each component placed in a separate food cup in the aluminum racks. They were given water ad libitum and were fed the vitamins daily. The four components, including the spillage, were weighed every two days, the fat and sugar each to a gram, the casein and salts each to a tenth of a gram. The cups were refilled, reweighed, and replaced in the cages, the order of their replacement being randomized each time. The animals were weighed every four days.

It was shown by Scott (8) and by Pilgrim (6) that not all rats select an adequate diet from the four components used in this experiment. In their experiments, as well as in this one, one-third to one-half of each group of rats failed to eat enough casein to permit adequate growth.

In this experiment, 22 of the animals were growing at a satisfactory rate and selecting an adequate diet at the end of three weeks of self-selection. Of the adequate selectors, which we will refer to as group I, some ate mostly fat and others mostly sugar; but all ate at least 3 gm. of casein every two days. The 21 animals that were not selecting an adequate diet were losing weight and ate very little, if any, protein. They appeared quite undernourished and had greasy hair, due most probably to not cleaning off accumulated fat. At this time (78 days of age), group I was continued on the four components, while the other animals were placed on a restricted diet consisting of only 1 gm. each of fat and sugar, with casein and salts ad libitum for each two-day period in order to determine whether or not they would eat casein and grow under these conditions.

All the animals on the restricted diet ate protein and began to grow, except one that died on the third day from a respiratory disorder and malnutrition. After 18 days of this diet these animals were again placed on the four-component self-selection diet. This part of the experiment was conducted in order to determine whether animals that did not previously eat casein would eat it if they were allowed only small amounts of the other two components supplying calories, and, further, whether they would eat it if again given a choice of the four components. The fact that the rats ate casein during the period of restriction of other sources of calories demonstrates that the need for calories, as described by Scott (8), leads to consumption of even a nonpreferred food. Even though this was not part of the original problem, it was felt that valuable information might be obtained from animals that would otherwise be destroyed.

At 100 days of age, and at the end of six weeks of self-selection, group I, consisting of 22 rats, was starved for two days except for access to water. They were then again allowed to select their diet from the four components. Three animals that were losing weight and not selecting adequately were eliminated at day 110; therefore, their results are not included in the analysis of the data. When the 20 animals which were on the restricted diet weighed approximately what they had before self-selection, they were put back on the self-selection diet. This was on day 96. At the end of two and one-half weeks of self-selection 10 of these animals were selecting adequately and growing (referred to as group II); the 10 which were not were eliminated. The ten animals of group II plus the 19 animals of group I were starved for a two-day period at 112 days of age. They were then put back on self-selection for a two-week period.

Statistical Analysis

Since there were no a priori reasons for assuming that the two groups could be combined, their data were analyzed separately. In fact, good reasons for not combining them existed; the restricted-diet group had only one period of starvation, and it was at an age different from the first starvation of group I.

The amounts in grams of the sugar, fat, and casein eaten by each animal were converted to calories, using the factors 3.87, 8.84, and 4.27 cal/gm, respectively. The amounts, in terms of calories, were also converted to percentage of total calories eaten by each animal. These values were averaged for all animals for each 48-hr. period of measurement.

The control period for group I begins with day 82, rather than day 61, because the earlier period of self-selection was used to accustom the rats to the situation as well as to determine which animals could select an adequate diet. For group II the control period begins on day 96 with the self-selection that followed the restricted diet.

An analysis of variance was run for group I in order to determine the significant changes and interactions in the experiment. Each of three components (fat, sugar, casein) was analyzed separately. The amount of calories eaten by each animal was divided into three periods,

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[3] The daily dosage provided the following amounts of vitamins:

thiamine hydrochloride	40 μg.	Vitamin A (acetate)	100 I.U.
riboflavin	40 μg.	Vitamin D (calciferol)	20 I.U.
pyridoxine hydrochloride	40 μg.	Vitamin K (2 methyl-1,4-naphthoquinone)	40 μg.
calcium pantothenate	200 μg.	Vitamin E (α-tocopherol)	400 μg.
nicotinic acid	200 μg.	biotin	1 μg.
choline chloride	10 mg.	folic acid	1 μg.
i-inositol	4 mg.		

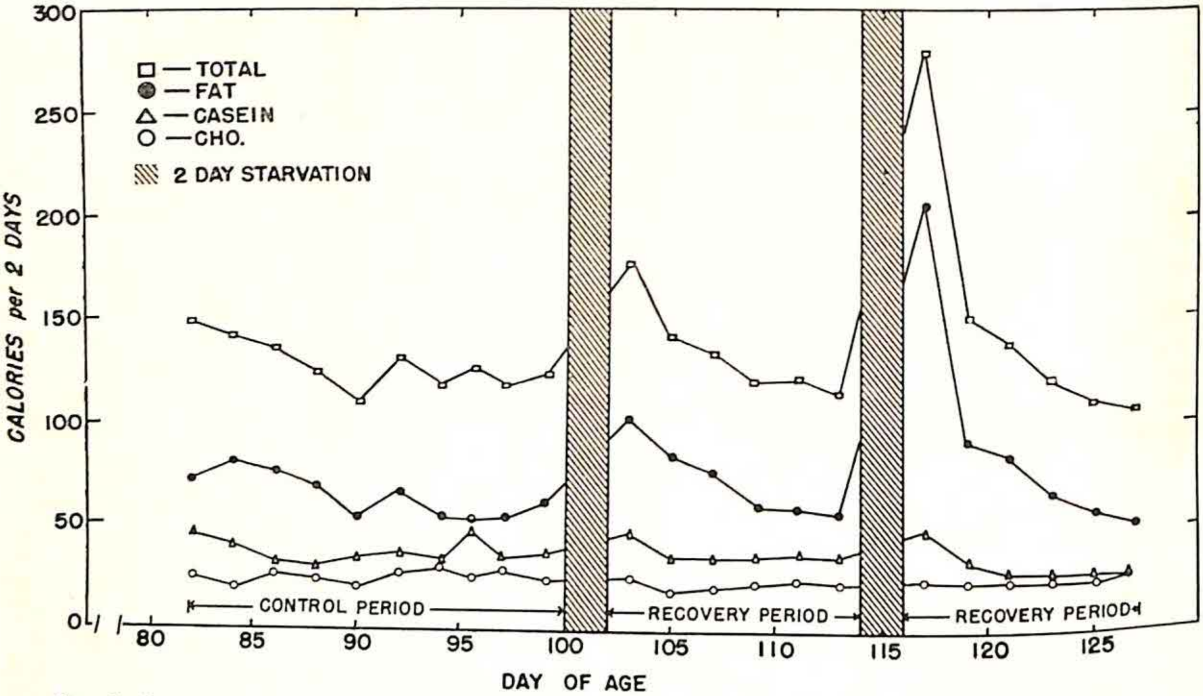

FIG. 1. Amount of calories eaten by group I, adequate selectors ($N = 19$) (CHO = carbohydrate)

one control and two recovery periods. The three periods were subdivided into three equally spaced subperiods, which consisted of the average of three values for each subperiod in the control period (a one-day weighing was omitted), and the average of two values for each subperiod of the two recovery periods. With these values a 3 by 3 by 19 analysis was run for each food component. In order to determine which period-subperiod differences contributed most to the significances that were found in the analyses, *t* tests were run using the method of differences (4).

RESULTS AND DISCUSSION

The group averages of caloric consumption of each component as well as total calories for days 82 to 127 for group I and for days 96 to 127 for group II are plotted in Figures 1 and 3. Each point represents caloric consumption for a two-day period. Figure 2 illustrates the data from Figure 1 converted to percentage of total calories. Although some have used this statistic, it should be noted that its use in the interpretation of these results is misleading in that the large increase in calories of fat consumed is automatically reflected as a decrease in percentages of sugar and casein even though the consumption, in terms of calories, of sugar and casein does not change. Actually, Figures 1 and 3 show that in both groups the amount of calories of fat consumed increased after starvation while the sugar and casein remained approximately the same.

Figure 4 illustrates the change in body weight for both groups throughout the experiment. The body weight of group I gradually increased throughout the experiment, except at the weighing period immediately after the second starvation when there was a slight decrease in weight. The weighing after the second starvation was done at the beginning of rehabilitation because it was noticed that no weight change was shown after the first period of starvation when weighing was done two days after rehabilitation was initiated. The body weight of group II decreased up to the time of the restricted diet, then there was a sharp increase up to the period of starvation, a small drop after starvation, and then a steady increase.

Although the patterns of changes after starvation generally are the same for both groups, they do differ in that: (*a*) more calories of fat are eaten by the restricted-diet group (group II), and (*b*) the adequate self-selectors (group I) obtain more calories from the protein than they do from the sugar, which is opposite from group II. A possible explanation of the first difference may be that group II is in a state of semistarvation when self-selection is reinitiated, and they make this up by eating more fat. This is suggested by a drop in fat consumption near the end of the experiment; presumably they have made up the deficit by

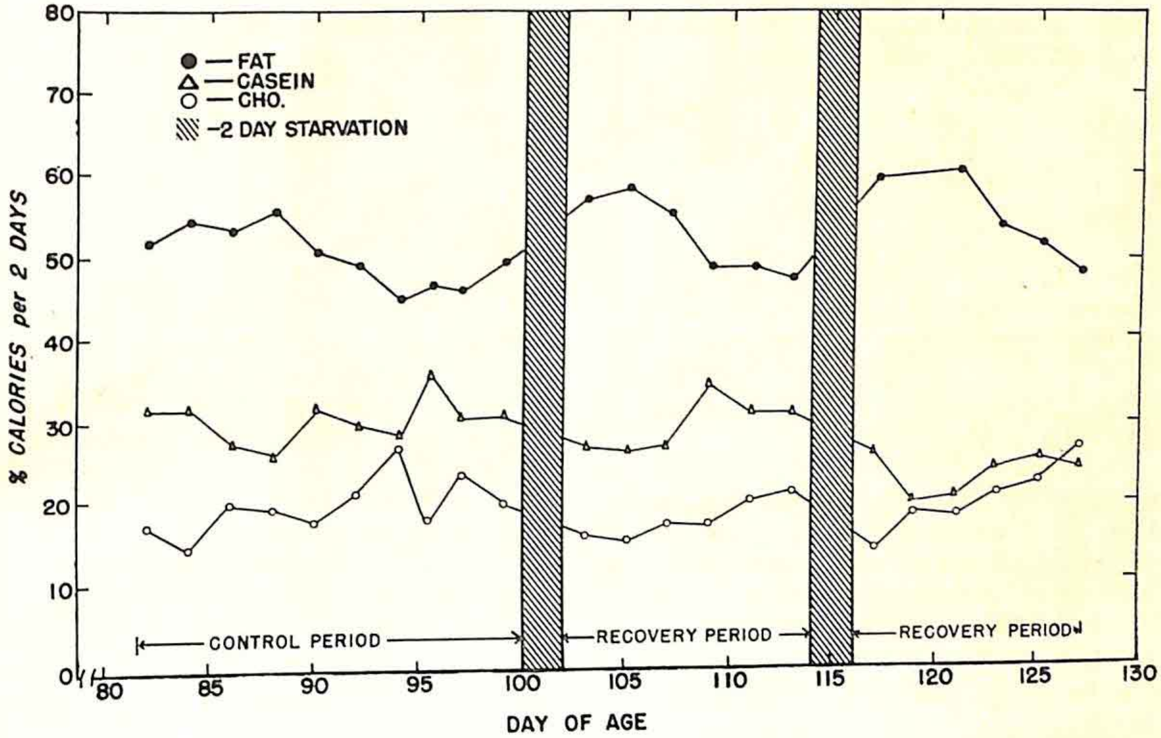

FIG. 2. Percentage of calories of each component eaten by group I, adequate selectors ($N = 19$) (CHO = carbohydrate)

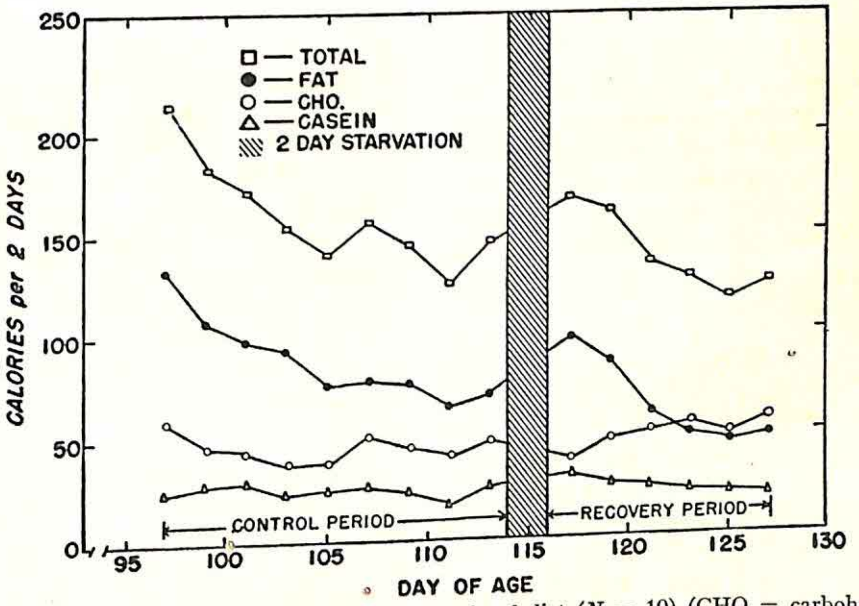

FIG. 3. Amount of calories eaten by group II, restricted diet ($N = 10$) (CHO = carbohydrate)

this time. Evidence for this is the fact that the average weight of group II (322 gm.) at the end of the experiment is almost the same as that of group I (337 gm.).

Results of the analyses of variance are shown in Table 1. The most meaningful effect is the period-subperiod interaction, for it represents the changes due to starvation. For this interaction the only significant result was in the fat analysis. All the effects were tested for significance against the mean square of the three-factor interaction.

The analysis of the data by t tests was utilized only when the analysis of variance

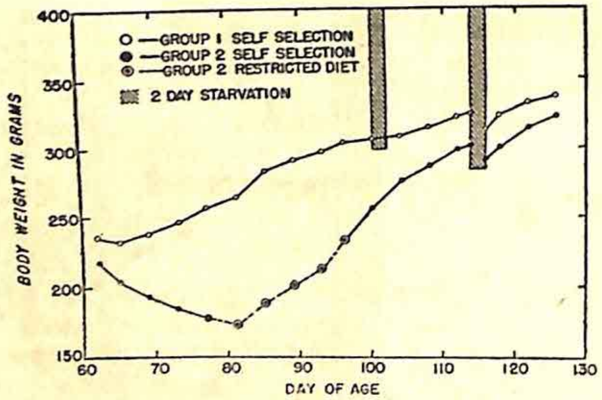

FIG. 4. Body weights of groups I and II (group I, $N = 19$; group II, $N = 10$)

indicated significant changes related to starvation. No t tests were run for carbohydrate since there were no significant effects that were related to starvation.

For fat, the average number of calories eaten by each rat during the control period was compared with each of the three subperiods following each starvation. Also, a t test was run between the first subperiods following each starvation to determine their role in the interaction significance since the caloric consumption after the second starvation is obviously greater than after the first.

The only significant t's were for the control period versus the first subperiods of the two recovery periods, which were significant at the .01 and .001 level, respectively, and between the two poststarvation subperiods at the .05 level. The former results indicate that the amount of calories obtained from fat is significantly different from the control period for only the four days after a starvation period. The latter result points to a possible learning effect due to the first starvation and recovery period, a fact which would fit into a theory of adjustment to repeated stress (9). The difference between the fat consumption after the first and second starvations can easily be seen in Figure 1. In line with this idea, the amount of calories of fat consumed by group II after their starvation, which comes at the same age as group I's second starvation, is very similar to that consumed by group I after its first starvation period (group I, 102.8 calories, and group II, 98.2 calories, for the two-day period following the first starvation). This similarity lends further support to the theory that there is some adjustment in the rat to the repeated stress of starvation.

For the data on casein, the same t tests as for fat were run but only to explain the main effects since the interaction related to starvation was not significant. The only significant t's were those between the control period and the second and third subperiods of the second recovery period, at which time there was a drop in casein consumption, as shown in Figure 1. These t's were both significant at the .05 level. Thus the only significant change in casein consumption over the experiment seems to be related to the factor of age.

SUMMARY AND CONCLUSIONS

The effect of starvation upon the pattern of self-selection by young adult rats of four purified dietary components, casein, fat, sucrose, and salts, has been described. The

TABLE 1

Analysis of Variance for Three Food Components

Source	*df*	Mean Square			*F* Values		
		Fat	Sugar	Casein	Fat	Sugar	Casein
Period	2	2859.25	91.50	595.31	7.09*	—	8.19**
Subperiod	2	18671.01	156.19	1218.71	46.33**	1.34	16.77**
Rat	18	10875.52	3594.89	2840.99	26.99**	32.30**	39.10**
P × S	4	1377.52	10.14	166.72	3.42*	—	2.29
R × P	36	1349.22	491.69	298.81	3.35**	4.23**	4.11**
R × S	36	484.72	125.71	815.73	1.20	1.08	11.23**
P × S × R	72	402.99	116.30	72.66			
Total	170	1996.28	563.79	437.40			

* Significant at the .01 level.
** Significant at the .001 level.

rats that could self-select satisfactorily (group I) were starved for two days and then placed again on self-selection for a recovery period, after which the procedure was repeated. Those that could not select satisfactorily were put on a restricted diet consisting mainly of casein and then placed on self-selection. The animals that could afterward select adequately (group II) were starved for two days at the same time as the second starvation of group I.

After a two-day starvation, rats did not show an avoidance for any particular food component, but rather a significant increase in the calories of fat consumed. Even when the dietary experiences of one group up to the time of starvation are quite different from those of another, both groups behave in a similar manner after starvation.

The need for calories will cause rats to eat a nonpreferred food, such as casein; and furthermore, some animals then continue to eat casein in a subsequent self-selection situation.

The repeated stress of starvation is followed by an adjustment which is represented in behavior by an increase in consumption of fat.

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Received February 17, 1954.

DEPRIVATION STATES AND BEHAVIORAL ATTRIBUTES

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Warner's findings that with 24-hr. deprivation thirsty rats would cross an electrified grid more often than hungry ones (3) have been interpreted to mean that 24-hr. water deprivation produces a "stronger drive" than the same number of hours of food deprivation. This has become a common interpretation in the literature. For example, Wickens, Hall, and Reid (4) recently invoked it to explain their experimental results. Such an interpretation of drives implies that different deprivation states (e.g., hunger, thirst) may differ quantitatively but have the same *qualitative* effect on behavior; that is, they "motivate" the organism. From this point of view, the progress of an animal's learning would not be intrinsically related to the specific deprivation used. Therefore, hunger or thirst would be equally valid deprivation states to use in any learning problem.

This paper will present an alternative proposition: that different deprivation states have different qualitative behavioral effects; i.e., they call forth different *kinds* of behavior. Such a proposal would be congruent with Krech's recent suggestion that we cannot treat motivation apart from other behavioral attributes. Thus, he writes, "... we [can] not talk about ... varying motivation and holding knowledge constant. Varying any one set of significant stimuli [e.g., nature of motivation] will vary *all* the attributes of behavior and experience" (1, p. 134). From this point of view, the specific nature of the deprivation state *is* relevant to the specific learning pattern which the organism must adopt.

In connection with another study, the authors conducted an experiment (part of which is reported here as Problem I) in which rats were required to acquire a simple position habit. Thirsty animals showed performance which was superior to that of hungry animals. However, the data disclosed a significant difference with respect to variability which could not be readily accounted for by any quantitative difference in motivation. If we were to hypothesize a qualitative difference in behavior, namely, that food deprivation produces greater variability in behavior whereas water deprivation produces greater stereotypy, then the above data could be readily understood.

To test the hypothesis that hungry rats are intrinsically variable in their behavior and thirsty ones stereotyped, Problem II, in which hungry and thirsty rats were required to adopt a response-alternation habit, was run. It was predicted that in this problem the hungry *S*s would show superior performance because of the greater variability of their behavior.

PROBLEM I

Subjects

The *S*s for this experiment were 78 male rats, approximately 100 days old, from the University of California colony.

Apparatus

The apparatus was an elevated T maze, painted a flat black, in which the runways were 2 in. wide, the main stem 68 in. long, and each arm 24 in. long. The goal boxes were 10 in. by 10 in. by 11½ in., and each was fitted with a one-way swinging door hinged at the top and slightly weighted at the bottom. The starting box, which was painted white, was 9 in. by 5 in. by 5 in. and was fitted with a guillotine door. The straightaway, starting box, and goal box used in the preliminary training were replicas of those in the T maze.

Procedure

Preliminary training. Each animal was handled approximately 5 min. a day for four days. At the end of the fourth day food was removed from the cages of half the animals and water from the other half. On the fifth, sixth, and seventh days the animals were placed for 5 min. in the straightaway goal box containing the appropriate incentive. Following this, each animal was run for four days (three trials a day) on the straightaway to the appropriate incentive. During this time the animals were gradually habituated to operating the door of the goal box. The animals were allowed to eat and drink ad lib. for 1 hr. in their home cages following the day's run.

T-*maze training.* After the preliminary training the animals ran 27 trials (3 per day). The first 6 trials were forced (trials 1, 2, and 4 rewarded; 3, 5, and 6 unre-

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[1] The authors are indebted to Professor Benbow Ritchie for his assistance in planning the research and to Professor David Krech for his assistance in preparing the manuscript.

TABLE 1

Trials to Criterion and Average Errors for the Learning Period for Both Groups

Group	N	Trials	σ_M	CR	Errors	σ_M	CR
H	42	14.6	0.52	3.2*	3.44	0.38	2.0**
T	36	12.4	0.45		2.31	0.43	

* Significant at the .001 level.

** Significant at the .02 level.

TABLE 2

Distribution of Errors

(Percentage of responses incorrect)

Group	N	Trial			Average
		1	2	3	
H	42	9.7	25.4	14.2	16.4
T	36	11.7	11.4	10.0	11.0

warded) to give the animals equal experience with the contents of the goal boxes. One goal box contained the appropriate goal object while the other contained nothing. The position of the correct goal box was *left* for half the animals and *right* for the other half. In this period the animals had the same motivation as in the preliminary training.

The animals were run using the noncorrection method with approximately 15 min. between trials. They were allowed 20 sec. for consummatory activity in the goal box after a correct response and were retained in the goal box for the same time after a wrong response.

Results

The data presented in Table 1 indicate that the thirsty animals were significantly superior to the hungry ones in terms of average errors over the learning period, as well as trials to criterion (10 correct choices over four successive days—12 trials).

Although the hungry group made more total errors than the thirsty group, there is an orderliness in the distribution of their errors (Table 2). The hungry group made more errors on the second trial of each day than the thirsty group (the difference is significant at better than the .001 level of confidence) but the two groups were comparable on the first and third trials. From this fact, and the differences between the two groups in trials to criterion and average errors, we would conclude that the thirsty group showed a strong tendency to stereotype its choice-point behavior and, for this reason, obtained "better" performance scores. The fact that the hungry animals ran faster than the thirsty ones and made as many correct responses on the first trial of each day suggests that the performance of the hungry group was not the result of "lower motivation."

PROBLEM II

Subjects

Twenty male rats from the University of California colony, approximately 110 days old, were divided into two groups of 10.

Apparatus

The apparatus used was the same as for Problem I.

Procedure

Preliminary training. This was same as for Problem I.

T-*maze training.* This was same as in Problem I except in the following respect: The first trial of each day was rewarded no matter which side the animal chose. However, on the second trial the reward was on the side opposite that chosen on the first trial. On the third trial the reward was located on the side opposite that which the animal chose on the second trial, regardless of whether trial 2 was correct or not. It can be seen that a position habit would result in only one rewarded response each day, i.e., one-third rewarded. Thus the problem was a simple *response* alternation. The time interval between trials for all animals was about 15 min.

Results

For the total 34 trials (scoring only the last 2 trials per day) the hungry group averaged 12.9 ($\sigma_M = 1.3$) errors while the thirsty group averaged 28.1 ($\sigma_M = 2.7$) errors. This difference is significant at better than the .0001 level of confidence.

The hungry group required a median of 23 trials to reach a criterion of 10 correct choices out of 12 trials. Only three out of the ten thirsty animals reached the criterion before the experiment was terminated, and these three required 28, 30, and 34 trials, respectively.

In this problem, also, the hungry group ran faster than the thirsty group. Performance curves for both groups on both problems are shown in Figure 1.

If the superior performance of the thirsty group on Problem I is interpreted as being an indication of a stronger "drive," a contradiction arises when Problem II is considered. In Problem II, the thirsty group's performance was significantly inferior to that of the hungry

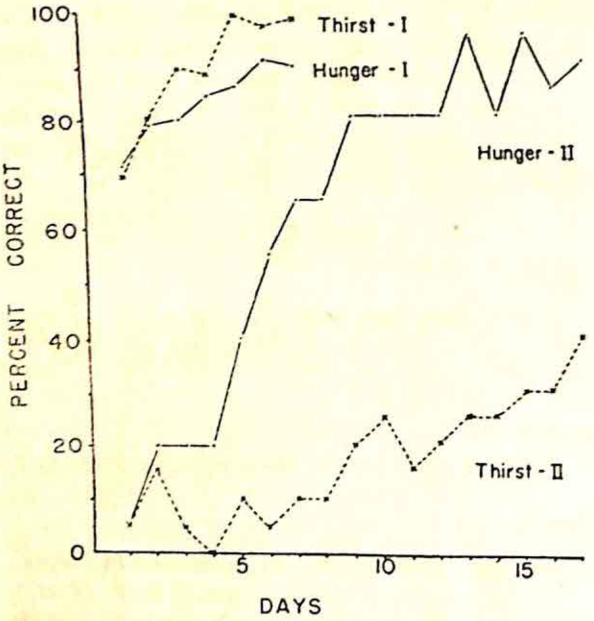

FIG. 1. Performance curves for Problems I and II

group, which would indicate that, in this problem, the thirsty group's "drive" was weaker. However, this interpretation is invalidated by the fact that the deprivation conditions were the same for both problems.

DISCUSSION

To interpret the above results we have proposed that the physiological conditions accompanying food deprivation produce a state of the organism which facilitates variability of behavior whereas those accompanying water deprivation produce a condition which facilitates stereotypy of behavior. This would lead hungry animals to make errors in learning a position habit, but would lead them into the correct response pattern in an experiment designed to take advantage of this variability and, conversely, would enhance the performance score of thirsty animals in learning a position habit while hindering their acquisition of an alternation habit.

One might speculate that this connection between hunger motivation and variability (and thirst and stereotypy) has biological survival value. Rats, although they are omnivores in the wild state, continually "explore" their environment to hunt food, whereas their water supply is presumably more fixed. Therefore, returning to the place where water was previously found is adaptive. But returning to where they last found food might not be as adaptive because of the uncertainties of food sources.

It would be expected that this sort of "hunger exploration" would be more evident in carnivores, because their food supply is constantly on the move, and less evident in those herbivores who have a more stationary food supply. One might therefore regard the variability difference between hungry and thirsty animals to be a manifestation of behavior patterns resulting from the evolutionary process of natural selection.

Quite aside from any "biological" argument, if one accepts the hypothesis that qualitative differences in deprivation produce qualitative differences in behavior, then it is necessary to re-evaluate references in the literature regarding variability of behavior. An example of this would be Krechevsky's paper on "Brain Mechanisms and Variability" in which he writes: "Variability in behavior is not only, or even primarily, an *effect* of a particular set of 'undesirable' environmental factors . . . but is rather a characteristic of animal behavior under almost any circumstances" (2, p. 140). And again, in describing his results, ". . . normal animals were [not] behaving in a 'random' fashion . . . the normal animal tended toward an *alternating* mode of response. . . . the normal animal showed no tendency to *fixate* the nonvarying path . . . " (2, p. 152).

However, in these studies Krechevsky used hungry rats. In the light of the present experiment, it is possible that his data do not pertain to "normal animals" but only to normal *hungry* animals. In general, our results suggest that in any study of variability or stereotypy in behavior the nature of the "drive" used must be carefully considered.

SUMMARY

Hungry and thirsty rats were run on a T maze in two problems. In one, animals were required to learn simply the location of a reward which was in a constant position. In the second problem animals were required to acquire a response-alternation habit. Thirsty animals excelled in the former, hungry animals in the latter.

We attribute these results to the fact that qualitatively different deprivation states have

qualitatively different behavioral effects. Specifically, we suggest that the physiological conditions accompanying food deprivation facilitate variability and those accompanying water deprivation facilitate stereotypy of behavior. The relationship of this suggestion to the problem of variability is discussed.

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responses (see reference 7 for a more complete discussion of this ratio). It expresses the difference in output between the first and second 3-min. segments of the curve as a fraction (percentage in decimal form) of the output during the first 3-min. segment. (The "inflection ratio" = $B - A/A$, where A is the number of lever responses made during the first and B is the number made during the second 3-min. segment of the curve.) Complete cessation of lever pressing during the clicker (or second 3 min. of the curve) appears as a ratio of −1.00, essentially unchanged output appears as a ratio of around 0.00, and a 100 per cent increase in output appears as a ratio of +1.00.

The −1.00 "inflection ratio" value for group I indicates complete post-ECS retention of the CER. The values around 0.00 for group III, IV, and V, on the other hand, show the markedly attenuating effects of ECS treatments, administered anywhere from one per hour to one per day, upon the CER. For the animals in these three groups, the CS had lost its power to suppress the output of lever responses. Finally, the intermediate values of the inflection ratios found in groups II, VI, and VII indicate only moderate attenuation of the CER. For these animals the CS still retained some power to suppress lever pressing despite the fact that they had the same number of ECS treatments that had been given to all other groups.

DISCUSSION

The results of this experiment indicate quite clearly that the attenuating effect of a fixed number of ECS treatments upon an emotional response conditioned by a fixed number of acquisition trials varies considerably as a function of the concentration or distribution of the treatments in time. The attenuating effect of ECS upon the CER is markedly reduced if the treatments are spaced as far apart as 48 hr. or more, or if they are concentrated as closely together as ½ hr. or less. Furthermore, the ECS fails to have any demonstrable attenuating effect upon the strength of the CER if the treatments are so closely concentrated that the animal receives, in effect, only one convulsion. Each animal of group I, given 21 single ECS stimulations in 21 sec., showed only one convulsion, while several animals of group II, given one ECS treatment every ½ hr., did not have all 21 convulsions. The retention of a strong CER in these two groups during the post-ECS retention test is consistent with previous experimental demonstrations (4, 8, 9) of the critical role played by the convulsions in the attenuating effect of ECS upon the CER.

Clearly, however, considerations relative to the number of convulsions alone do not account for all the variance between groups in the present experiment. Indeed, all animals in groups VI and VII (which showed retention of a strong CER during the post-ECS retention test) had 21 full-blown tonic-clonic convulsions as a result of the ECS treatments. The temporal dispersion of the treatments in these two groups, however, appears to have considerably reduced their effectiveness in attenuating the CER.

At least two possible explanations for this finding present themselves. First, previous research (2) has indicated that the CER tends to increase in strength with elapsed time alone. This suggests that 21 ECS dispersed over a one- to two-month period may be less than maximally effective in attenuating a response grown stronger with time in these groups. A second possible explanation may be that the ECS treatments derive their effectiveness from the cumulative physiological consequences of the convulsion. If this were the case, delays of 48 hr. or more between treatments, permitting considerable recovery from immediate post-convulsive physiologic changes, would tend to reduce such cumulative effects and leave the CER only minimally affected. Indeed, some support for this latter hypothesis is to be found in the consistently higher attrition rates following ECS (due to vertebral fractures, transactions of the spinal cord, general debilitation, etc.) found in animals receiving concentrated doses of ECS (groups I, II, and III). No such losses occurred in groups VI and VII. Furthermore, had the convulsions in these latter two groups been maximally effective in the physiological sense, they could have been expected to counteract any normal increase in the strength of the CER. Certainly, the animals in group V showed virtually complete attenuation of the CER even though the ECS treatments were spread over a period (21 days) during which significant increases in the strength of the emotional response have been shown to occur (2). It is clear, however, that the effects of interaction between increases in the strength of the CER with time and dissipation of the cumulative physiological consequences of the convulsions with extended intertreatment intervals still remain to be explored in further experiments.

SUMMARY AND CONCLUSIONS

The present experiment investigates the magnitude of the effect of electroconvulsive shock (ECS) upon a conditioned emotional response (CER) of the "fear" or "anxiety" type, as a function of the temporal distribution of the ECS treatments.

Eighty-four male albino rats were trained in lever pressing and received eight emotional conditioning trials, each consisting of a 3-min. presentation of a clicking noise terminated contiguously with a shock to the feet. Then the animals were divided into seven groups (12 rats each) and received 21 ECS with a different time interval between treatments (1 sec., ½, 1, 8, 24, 48, and 72 hr.) for each of the seven groups, respectively.

Two days after the last ECS treatment for each group, all animals were tested for retention of the CER. The ECS had no discernible effect on the CER in group I (one ECS every second) but did partially attenuate the CER in groups II (one ECS every ½ hr.), VI (one ECS every 48 hr.), and VII (one ECS every 72 hr.). But ECS had the greatest effect, completely or almost completely attenuating the CER, in groups III, IV, and V in which the animals received one ECS every hour, every 8 hr., and every 24 hr., respectively.

The results of this experiment indicate quite clearly that the attenuating effect of ECS upon the CER is in part a function of the temporal distribution of the ECS treatments. The range of optimal effectiveness appears to be between one ECS every hour and one ECS every 24 hr., with treatments administered more or less frequently producing less attenuation of the CER.

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Received July 29, 1954.
Early publication.

THE EFFECT OF A SERIES OF ELECTROCONVULSIVE SHOCKS ON WEIGHT CHANGE IN THE MALE ALBINO RAT

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A number of authors have pointed out that when albino rats are subjected to a series of electroconvulsive seizures, one of the observable changes is an alteration in the animal's body weight. The findings in general have indicated that when the male albino rat is subjected to a long series of ECS (8), it loses weight during the first 10 ECS treatments, shows some increase in weight from treatment 10 through 90, and then rapidly loses weight, death ensuing somewhere between treatments 90 and 150. When between 10 and 30 daily ECS were administered, investigators generally found a loss in weight during the first 10 to 15 ECS, and then either a gain in weight at a more rapid rate than found in control animals (1, 2, 7, 9) or a gain in weight less than or similar to a control group of animals (3, 4, 5, 6).

The present study investigated weight changes under two experimental conditions: (*a*) where animals were kept on ad libitum food and water schedules throughout the experiment, and (*b*) where animals were maintained on a 23-hr. deprivation schedule for both food and water prior to, during, and for a short period after administration of the last ECS.

METHOD

Apparatus

Shocks were produced by subjecting animals to an alternating current of 35 ma. for a period of 0.2 sec. Current was administered through modified alligator clips, good contact between pinnae and clips being maintained by use of electrolytic jelly.

Animals were weighed on a spring-type balance. Weight measurements were accurate to within 2 gm.

Subjects

Animals used were drawn from male stock maintained by the department of psychology of the University of Illinois. Two groups were used for the experiments under condition of deprivation. These were a group of 16 animals approximately 260 days old and a group of 16 animals approximately 100 days of age at the start of the experiment. Twenty-two animals that were approximately 120 days old at the start of the experiment were utilized in the experiment where animals were kept on an ad libitum feeding regimen. Food used was dry Purina Lab Chow pellets.

Procedure

Each of the three groups of animals was divided into a control and experimental group, each control group being subjected to the same procedures as the experimental animals with the exception that they did not receive convulsive seizures. Older animals in the food- and water-deprivation series were placed on the deprivation schedule 14 days before the first ECS was administered, while younger animals were placed on deprivation schedules 9 days prior to the first ECS treatment and were maintained on this schedule throughout the period of ECS administration and for a short period thereafter. They were then returned to an ad libitum food and water schedule and observed for an additional number of days. Different periods of preshock deprivation schedule between the old and young animals were utilized because it took the old animals longer to adapt to the deprivation schedule in terms of weight stabilization, i.e., they lost considerable weight during the first 3 to 4 days of the experiment; the young animals did not show such an initial weight loss. The procedure for administration of ECS and feeding for these animals was as follows: Animals were removed from their home cages and weighed, were then introduced into individual feeding boxes, and remained in these boxes for 1 hr.; they were then returned to the room in which they were housed, were again weighed, and returned to their home cages. These procedures were performed between the hours of 7 to 9 A.M. During the period of administration of ECS, animals were removed from their home cages between 7 and 9 P.M. and subjected to the convulsive procedure, current being applied only to animals in the ECS group. Animals were subjected to a series of 16 ECS administered at the rate of one per day for a total of 16 days. Animals were placed in individual cages for approximately 1 hr. after ECS to recover from the effect of the convulsive seizure and then were returned to their home cages. After the animals had returned to an ad libitum feeding schedule, they were weighed daily between the hours of 7 and 9 P.M. The group of animals maintained on ad libitum feeding schedule throughout the experiment was weighed between the hours of 7 and 9 A.M. and was convulsed between the hours of 7 and 9 P.M.

RESULTS

Since our prime interest was in weight changes occurring as a function of a series of ECS, our data were analyzed in terms of daily weight changes for each animal. Comparisons made were between the experimental and control groups in each of our experiments. Analysis was made in terms of the number of animals in each group losing weight from one day to the next. This information was then grouped into nine- or ten-day intervals (9 to 10 days pre-ECS; first 10 days of ECS; last 6 days of ECS plus the next 4 post-ECS days; and a 10-day post-ECS period). These periods were utilized for comparison because the findings of other investigators indicated that animals generally lost weight during the first 10 ECS treatments and then started to gain weight. The critical period under investigation thus was the first 10 days of the ECS period, with the other periods acting as controls.

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[1] These experiments were conducted in the psychological laboratory of the University of Illinois.

Statistical analysis utilized the Mann-Whitney *U* test. Table 1 presents our findings. A similar analysis was made in terms of mean weight change per group from day to day. The results of this analysis are consonant with the results of the above analysis and will therefore not be presented.

As is apparent from our graph, and as was borne out by statistical analysis, the control animals in group A were significantly heavier than the experimental animals at the start of the experiment. This finding accounts for the one significant difference found in the comparison between these two groups of animals. The heavier control animals initially lost more weight than the lighter experimental animals, hence the significant difference between the pre-ECS comparisons. When the effect of weight was partialed out by using a ratio of weight change over mean weight, this significant difference disappeared, and no significant differences between the two groups of animals were found. A similar analysis was conducted for the group B experiment since a tendency toward a significant difference was found in comparing the control and experimental animals during the period of ECS administration. Again no significant differences were found. The significant difference between experimental and control animals of the group maintained on ad libitum feeding schedule during the period of administration of the first ten ECS is in agreement with the finding of other investigators.

TABLE 1

Analysis of Weight Change in Terms of Number of Animals per Day Losing Weight

Group	9 to 10 Days Pre-ECS	First 10 Days of ECS	Last 6 Days of ECS and Next 4 Days	Next 10 Days Post-ECS
A	0.02*	0.4	0.5	0.5
B	>0.5	0.1	>0.5	0.5
C	>0.5	0.01*	>0.5	0.3

* Significant beyond the .02 level.

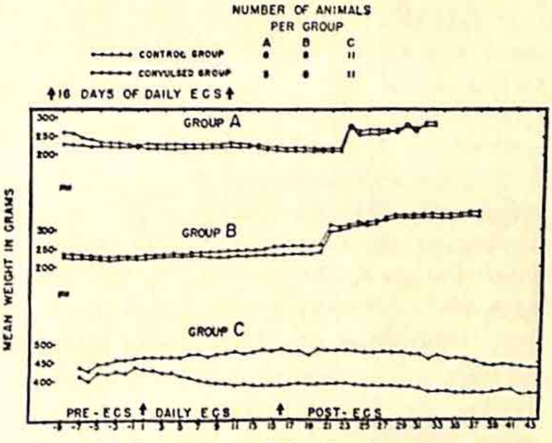

FIG. 1. Daily mean weight for the three groups (group A—old animals maintained on deprivation schedule; group B—young animals maintained on deprivation schedule; group C—young animals maintained on ad libitum feeding schedule throughout the experiment)

Figure 1 presents the daily mean weight data for the three groups (group A—older animals maintained on deprivation schedule; Group-B—younger animals maintained on deprivation schedule; group C—adult animals maintained on ad libitum feeding throughout the experiment). Three animals died during the experimental series; all of these were in group A and were part of the ECS series. One died after the fourth ECS; the other two after the ECS series had been completed. None of the animals that died during the course of the experiment was included in the weight analysis shown in Figure 1. As can be seen from Figure 1 (A and B), as well as from the statistical analysis, a series of ECS administered to animals on deprivation schedules does not affect their weights as compared with those of a control group; similarly, when animals are returned to an ad libitum feeding schedule, convulsed animals gain weight and stabilize at the same weight level found for nonconvulsed animals. These findings are true for animals that have attained a relatively stable weight level at the start of the experiment (group A) as well as for animals that were still gaining weight when the experiment was started (group B). Animals maintained on ad libitum schedule show weight changes akin to those reported by a number of authors (3, 4, 5, 6). As indicated in Figure 1 (C), the convulsed animals started to lose weight after the first convulsion and continued to lose weight through the ninth convulsion, leveled off at approximately the tenth convulsion, and maintained themselves at this weight level throughout the remainder of the experiment.

DISCUSSION AND CONCLUSIONS

The findings of these experiments indicate that a series of ECS will effect weight changes in male albino rats under specific conditions, i.e., where animals are kept on ad libitum feeding schedules. Where animals are kept on a 23-hr. deprivation schedule, they maintain themselves at the same weight level as control animals and show weight gains comparable to those of control animals when taken off the deprivation schedule. Water and food intake were also measured for the animals maintained on the deprivation schedule. Measurement of water and food intake indicates that the series of ECS had altered neither water nor food intake of the convulsed animals as compared with the control group. Similar information was not available for our animals maintained on the ad libitum feeding schedule (group C). Politzer (6), however, found that both food and water intake is decreased during the early phases of a series of 25 ECS administered at the rate of one ECS per day; that after about 9 ECS food and water intake slowly begins to increase; and that after completion of the series of ECS both food and water intake of the experimental group is larger than that of the control group, although the experimental animals maintained themselves at a weight level below that of the control group throughout the experiment.

One of the interpretations of the weight changes occurring during a series of ECS has been cast within the conceptual framework of Selye's General Adaptation Syndrome (1, 8). The daily convulsive seizures are considered to be the stressor agent to which the organism reacts adaptively. The weight changes are considered as one of the nonspecific systemic reactions; the stages through which the GAS develops are reflected in the weight changes. Since we consider both a series of ECS and systematic food deprivation to be stressor agents, it might be more advisable to superimpose the food-deprivation stress on the ECS stress since we have more information about the stages of adaptation the animal is in after a given number of daily ECS has been administered. We hypothesize that animals enter the countershock stage roughly between ECS 5 and 15, are in the resistance stage between ECS 16 and 90, and in the stage of exhaustion from ECS 91 until death. Effect of crossed stress (food deprivation) should have a differential effect on the nonspecific response (weight change), depending on where it is introduced. Theoretically, if introduced during the countershock stage, it should affect ongoing weight changes little; during the resistance stage it should produce more of a weight loss than it did when introduced during the countershock phase; and if introduced early in the exhaustion stage, it should hasten death. Adaptation to the stressor agent is indicated by the leveling off of the weight curve somewhere between convulsion 8 and 12 and an increase in weight generally occurring before the series of ECS is completed. As Riess has shown, when the series is extended to above 90 ECS, the animals again start losing weight, become generally debilitated, and are considered to have reached the exhaustion stage of the GAS. The findings for our animals kept on a deprivation schedule and subjected to ECS while on such a schedule may also fit into this framework if we consider the deprivation schedule as a stressor agent. We would hypothesize here that our animals (which had been on the deprivation schedule for a period of 9 or 14 days prior to the first ECS) had started to adapt to this stress, i.e., were in the "countershock" phase, and that the "adaptability" of the organism was "mobilized" so that general resistance to stress in general was raised. A crucial experiment to test this application of the GAS theory would be to subject the animals to a deprivation schedule for a longer period of time so that they can be assumed to have passed into the "stage of resistance" during which the animal is more highly resistant to the specific stressor agent (food deprivation in this case) and would become less resistant to other damaging stimuli, i.e., a series of ECS. We would then expect our animals to lose weight during the series of ECS. We feel that this theory adequately accounts for the above finding. Until experiments elaborated above are performed, we feel that research within the framework of this theory will prove to be fruitful.

SUMMARY

This experiment was designed to measure weight changes in male albino rats subjected to a series of ECS administered at the rate of one per day for 16 days under two experimental conditions: (*a*) where animals were maintained on ad libitum food and water schedules throughout the experiment, and (*b*) where animals were maintained on a 23-hr. deprivation schedule for both food and water prior to, during, and for a short period after administration of the last ECS. Results indicate that under conditions of ad libitum feeding animals lost weight between the first and ninth convulsion, weight leveled off after approximately ten convulsions, animals maintaining themselves at approximately this weight level for the remainder of the experiment. Animals subjected to a series of ECS under conditions of food and water deprivation do not show any difference in weight change when compared with control animals either during the period of deprivation or upon return to ad libitum feeding conditions. The findings are interpreted within the framework of Selye's General Adaptation Syndrome.

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Received February 12, 1954.

FORCE OF RESPONDING DURING EXTINCTION AS A FUNCTION OF FORCE REQUIREMENT DURING CONDITIONING[1]

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Two articles (1, 3) have recently criticized experiments designed to test the fatigue (5, 6) or reactive inhibition (2) theories of extinction because these experiments failed to control "habit strength"—specifically, force requirement per response during conditioning. According to this criticism, two studies (6, 7) interpreted as supporting fatigue or inhibition theories of extinction may be regarded as demonstrating that requiring forceful responses during conditioning yields forceful responses during extinction. It is a further implication of this criticism that if a reinforcing stimulus is made contingent on weak responses, then weak responses should occur during extinction.

It was the purpose of the present experiment to determine the validity of both these hypotheses. Specifically, it was expected that force requirement during conditioning would be positively related to forcefulness of responding during extinction. Conditioning with a moderate force requirement per bar-pressing response in rats should yield more *incomplete* bar presses during extinction than conditioning with a heavy force requirement. Conversely, conditioning with a heavy force requirement should yield more *complete* bar presses during extinction than conditioning with a moderate force requirement.

METHOD

Subjects and Apparatus

The *S*s were 16 experimentally naive male albino rats of Wistar stock maintained by the psychology department of Brown University. Their mean age was 79 days (range, 72 to 86) at the start of taming.

The apparatus consisted of a wooden box 12 in. by 12 in. by 5 in. deep, with a hinged glass front and a ½-in. hardware cloth floor. The bar assembly consisted of a rectangular brass frame 5½ in. by 1¼ in. by ¼ in. thick; it was pivoted at its center and extended ½ in. into the right end of the box 4½ in. above the floor. The gram mass required to depress the bar could be varied by hanging weights on the exterior end of the bar assembly. An electrically heated wire was attached to the end of the bar, and recorded all vertical movements of the bar on wax paper which moved at constant speed. Depression of the bar closed a mercury cup switch, activating a solenoid-operated food delivery mechanism, which delivered a dry food pellet into a food cup fastened to the floor below the bar. The distance the bar had to move to activate the food-delivery mechanism could be varied from a fraction of a centimeter to over 1 cm. A leaf-spring stop prevented bar depressions of more than 1½ cm.

Procedure

Half the *S*s were conditioned with a moderate force requirement (50 gm.), and half with a heavy force requirement (100 gm.). Half of each conditioning group was extinguished with a 50-gm. force requirement, half with a 100-gm. force requirement. In terms of force requirement during conditioning and extinction, respectively, the four groups which comprised the experiment were: 50-50, 100-50, 50-100, and 100-100. With age balanced, *S*s were assigned randomly.

Taming (*12 days*). The *S*s were handled and fed (8 gm/rat/day) at the same time each day.

Conditioning (*12 days*). Each *S* was permitted to make 20 food-reinforced bar presses per day. On day 1 a 10-gm. force was required to depress the bar the ½ cm. necessary to activate the food-delivery mechanism. Conditioning on the first day was facilitated by the presence of several food pellets on the bar and in the aperture through which the bar protruded, and by *E*'s completion of bar presses which approached ¼ cm.

On days 2 through 4 the minimal excursion of the bar necessary for food delivery was gradually increased to 1 cm. On days 5 and 6, the force required for a 1-cm. bar press was increased stepwise. For the 50-gm. conditioning groups, there was a 4-gm. increase every fourth bar press to 25 gm. on day 5, and about a 6-gm. increase every fourth bar press on day 6. On these same two days, the force required of the 100-gm. conditioning groups was increased to 50 and 100 gm. by 10- and 12½-gm. steps. Thus, at the end of 12 days of conditioning, each *S* had made 124 food-reinforced bar presses which required a minimal force of 50 or 100 gm., after having made 116 bar presses of lesser force requirement.

A dry food pellet weighing about 0.04 gm. was used as a reinforcing stimulus. Supplementary feeding came at least 2 hr. after the end of each *S*'s daily session. Thus *S*s were run after 19 to 21 hr. of food deprivation. For supplementary feeding *S*s were given access to Purina Lab Chow pellets for 1 hr. without water.

Extinction (*two days*). The *S* was placed in the apparatus for a 10-min. period each day. The food-delivery mechanism was disconnected to eliminate auditory secondary reinforcement due to its activation. Similarly, use of the leaf-spring stop on the bar, it was hoped, would minimize secondary reinforcement due to

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[1] This experiment constitutes a portion of an M.S. thesis carried out by the second author under the first author's direction.

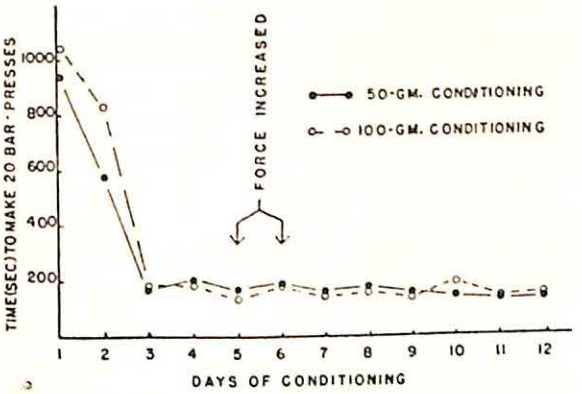

FIG. 1. Course of conditioning with 50-gm. and 100-gm. force requirements

sudden stopping of the bar. Supplementary feeding was the same as during conditioning.

One *S* in the 50-50 group was run only on the first extinction day. Accordingly, the 50-50 group will have an *N* of 3 whenever data for both extinction days are lumped or whenever data for day 2 alone are being considered, but an *N* of 4 whenever data for day 1 alone are being considered.

The recording of bar presses during extinction was such that both *incomplete* responses (i.e., bar presses greater than 1 mm. and less than 1 cm.) and *complete* responses (i.e., 1-cm. bar presses that would have produced food during conditioning) could be separately analyzed.

RESULTS

Conditioning

The course of conditioning of the two force groups is shown in Figure 1. Mean total time to make 20 bar presses is plotted on days. It is apparent from the figure that the gradual increases in bar weight produced no differential break in the performance of the two groups.

Extinction

Table 1 summarizes the responding during extinction, broken down by days of extinction. In terms of incomplete responses on day 1, the direction of differences is as expected. Thus, the 50–50 group responded incompletely more frequently than the 100–50 group, and the 50–100 group responded incompletely more frequently than the 100–100 group. Taken alone, neither difference is statistically significant when the group measures are analyzed by the Mann-Whitney nonparametric rank test (4). However, when the differences are evaluated according to Wilcoxon's (8) technique for grouping data, the p is .015 for both tails of the distribution of rank differences.

TABLE 1

Median Bar Presses during Each Extinction Day

Group*	Day 1		Day 2	
	Complete R's	Incomplete R's	Complete R's	Incomplete R's
50–50	55.5	8.5	20.0	4.0
100–50	54.0	2.0	34.0	2.5
50–100	29.0	20.5	13.5	15.0
100–100	31.5	9.0	17.5	4.0

* On day 1, *N*, per group = 4; on day 2, *N*, 50–50 group = 3; *N*, other groups = 4.

On day 2 the incomplete responding of three of the groups was similar and negligible, while that of the 50–100 group was still quite frequent. The difference between the 50–100 group and 100–100 group has a p of .04, both tails, according to the Mann-Whitney test.

Combining the incomplete responding for both days (Table 2), we find that 50-gm. conditioning produced significantly more incomplete responses than 100-gm. conditioning. The p is .04, both tails, according to Wilcoxon's grouped data test and .01 according to an analysis of variance F test performed on a square root transformation of the data.

For complete responses only day 2 of extinction shows statistically significant differences in line with expectation. Here the 100-gm. conditioning groups responded completely more frequently than the 50-gm. conditioning groups (p of .02, both tails, according to Wilcoxon's grouped data test).

Table 2 also shows that the 100-gm. extinction groups made fewer complete responses than the 50-gm. extinction groups during the two days of extinction combined. The p for this difference is .05 according to Wilcoxon's

TABLE 2

Median and Mean Bar Presses for the Two Days of Extinction Combined

Group*	Complete R's		Incomplete R's		Total R's	
	Median	M	Median	M**	Median	M
50–50	79.0	80.3	10.0	11.3	89.0	92.3
100–50	88.0	94.0	5.0	5.1	93.0	99.2
50–100	44.5	43.5	35.5	32.4	74.0	79.0
100–100	49.0	59.5	14.5	15.0	62.0	74.8

* *N* = 15; *N*, 50–50 group = 3; *N*, other groups = 4.

** The figures in this column are squared means of square root transforms of the data.

values in terms of the relationship it bore to the no. 4 gray on the bottom half of the card. "Darker than" should be associated with jumping left, and "lighter than" should be associated with jumping right. Consequently, if this reference gray, no. 4, were now shifted up or down the brightness continuum, S's reactions to the other six grays should change in accordance with the shift in relationships resulting from this change in the reference stimulus. It is in this sense that we can speak of transposition behavior in this situation.

The differential predictions made by the two theories for this type of transposition can be illustrated as follows. Suppose that during the test trials the top half of the two cards was gray no. 2 and the bottom half was gray no. 3. The specific stimulus theory would predict a jump to the right because both grays had previously been associated with such behavior. Similarly, the relational theory would predict a jump to the right in that the top half was lighter than the bottom half. Both theories would predict the same on such a test. On the other hand if the top half was gray no. 3 and the bottom half was gray no. 2, the specific stimulus theory would still predict a jump to the right for the same reasons as in the previous case, but a relational theory would predict a jump to the left because the top half was now darker than the bottom half. Thus the two theories would make directly opposing predictions on such tests.

It is apparent that several such test pairs leading to differential predictions by the two theories are possible among this set of stimuli. Consequently, this type of transposition experiment should provide a fairly clear-cut answer to the question of whether or not it is necessary to assume that relational responding is a fundamental form of behavior.

METHOD

Subjects

The Ss were 12 albino rats between 60 and 90 days old at the beginning of the experiment. They were tamed and then placed on a food-deprivation schedule during which they were allowed to eat all the food they wanted for 2 hr. each day. This schedule was started two weeks prior to the experiment and continued throughout the training and testing.

TABLE 1

Reflectances of Seven Grays as Measured by the Illumitronic Engineering Reflectometer

(The illumination of these when in position was 2.5 to 3.0 ft.-candles.)

Gray	Reflectance	
	%	Log.
1	73.0	1.863
2	43.0	1.633
3	30.0	1.477
4	20.0	1.301
5	15.5	1.190
6	9.5	0.978
7	7.0	0.845

Apparatus

The apparatus was a modified Lashley jumping stand painted a flat black. The windows were 7 in. by 9 in. The jumping platform was 8 in. from the windows and at a height such that S's head was on the same plane as the mid-point of the two cards. The back of the platform from which Ss jumped consisted of a box, 12 by 12 by 12 in. The front wall of this box was of milk glass. A 100-w. lamp inside the box provided all the illumination for the apparatus. Because of the diffusion of the light through the milk glass, an even illumination of the two cards without shadows was obtained even though S stood in front of it.

The seven stimulus grays used were obtained by mixing various proportions of flat black and flat white paint, and then painting a large quantity of paper with each mix. In this way several cards all of a constant gray value could be obtained. An attempt was made to have equal brightness steps between adjacent grays in the series, but as the reflectance values in Table 1 indicate, this equality was not obtained. Stimulus cards were made from these gray papers by covering the top half of the card with one gray and the bottom half with a different gray.

Procedure

The Ss were adapted to the apparatus by first feeding them on it, then teaching them to jump the gap to an open window, and finally to jump the gap when the windows were closed by stimulus cards of gray. Each S was then given a "dry run" of 20 trials to these neutral cards during which either the right or left window was blocked in random order. If it jumped to the blocked one, S was placed back on the jumping stand and forced to jump again until it chose the open one. It was hoped by this method to break the animals of position preferences and to adapt them to the type of punishment involved. However this procedure seemed to result in partial fixations for some Ss. During this adaptation period, as well as the remainder of the training and testing, S was never forced to jump by beating its tail or similar methods; S was always left on the stand until it had initiated its own choice. It appeared that the heat and light coming from the box behind *S* increased the motivation to jump even when a series of punishments had occurred on the preceding trials.

The training of *S*s was in two stages. During the first stage only two different stimulus cards were used. They were 1/4, i.e., the top half was gray no. 1 and the bottom half gray no. 4, and 7/4. On a given trial both cards were exactly the same. The *S*s were rewarded if they jumped to the right when the top half was lighter than the bottom and if they jumped to the left when the top half was darker than the bottom. Otherwise they were punished by a blocked window and fell to a platform below the apparatus. Training was by a correction method; if *S* made a mistake, it was immediately picked up and forced to jump again until it made a correct choice. A trial consisted of one rewarded response. The stimuli were so arranged that not more than two jumps to the same side occurred on consecutive trials. Half the jumps were to the right and half to the left. Five trials a day, spaced at 20- to 30-min. intervals, were given until *S*s reached a criterion of 9 out of 10 consecutive correct responses. If upon reaching the criterion, any *S* was not jumping readily and directly at the stimulus card, it was given additional training until this condition was corrected.

During the second stage of training, all *S*s were presented with the following set of six stimuli: 1/4, 2/4, 3/4, 5/4, 6/4, and 7/4. These stimuli were presented in six different orders with the restriction that not more than two jumps to the same side succeeded each other on consecutive trials. Again *S*s had to jump right when the top half was lighter than the bottom half and to jump left when it was darker. Training was continued for 30 trials, with five trials per day. If by that time *S* had not reached a criterion of going twice through the sequence of six without error, training was continued until *S* did reach it. One of the 12 *S*s showed such a strong position preference that it was discontinued before the test trials.

During the test period five trials a day were given; three were a continuation of the previous training trials and the other two were test trials. On the test trials both cards were unlocked and *S* was rewarded regardless of which way it jumped. The 24 test stimuli used are shown in Table 2. The following restrictions were imposed on the test stimuli: (*a*) each *S* went through the 24 stimuli in a different order; (*b*) on a given day 22 different stimuli were tested; (*c*) the two test stimuli presented to *S* on a given day were of such a nature that if the animal jumped relationally, one of the jumps would be to the right the other to the left, with the right jump occurring first on half the days and the left occurring first on the remainder; (*d*) the test trials were given on the third and fifth trials of each day and so interspersed with the training trials that if *S* reacted relationally to the test stimuli, it would never be rewarded more than two consecutive trials on the same side; and (*e*) the pair of stimuli presented on a given day always had the same number of brightness units between the two grays, e.g., 1/2 and 6/5 or 3/5 and 7/5.

Five *S*s, picked at random, were given posttest training on a successive discrimination. It was assumed that if *S*s had been reacting to the specific stimulus values, rather than relationally, they should be able to discriminate between grays no. 3 and 5 even though the reference value no. 4 was absent. They had done so during the original training trials when the bottom half of each card was gray no. 4. Consequently, each of these *S*s was trained for 50 trials, 5 trials a day, on a successive discrimination involving grays no. 3 and no. 5. When both cards were no. 3, they had to jump right; when both were no. 5, they had to jump left. Rewards and punishment were correlated with these jumps in the same manner as during the original training.

RESULTS

In order to reach the criterion of 9 correct out of 10 consecutive trials on stimuli 1/4 and 7/4, *S*s required on the average 31.5 trials. With the overtraining given them, they averaged a total of 60.8 training trials on these stimuli. When transferred to the training stimuli 1/4, 2/4, 3/4, 5/4, 6/4, and 7/4, they required an average of 7.6 trials to reach the same criterion of 9 correct out of 10 consecutive trials. This indicates a considerable amount of transfer. Each *S*, however, was continued on these stimuli for at least 30

TABLE 2

Frequency of Relational Responses to 24 Test Stimuli

Difference in Brightness between Grays	Stimulus and Response	Gray on Bottom Half of Card						%
		No. 1	No. 2	No. 3	No. 5	No. 6	No. 7	
	Stimulus	2/1	3/2	4/3	6/5	7/6		
+1	Relational	8	7	8	10	11		80
	Nonrel.	3	4	3	1	0		20
	Stimulus		1/2	2/3	4/5	5/6	6/7	
−1	Relational		10	9	3	5	2	53
	Nonrel.		1	2	8	6	9	47
	Stimulus	3/1	4/2	5/3	7/5			
+2	Relational	9	10	10	11			91
	Nonrel.	2	1	1	0			9
	Stimulus			1/3	3/5	4/6	5/7	
−2	Relational			11	11	10	6	86
	Nonrel.			0	0	1	5	14
	Stimulus	4/1	5/2	6/3				
+3	Relational	10	10	11				94
	Nonrel.	1	1	0				6
	Stimulus				2/5	3/6	4/7	
−3	Relational				11	10	8	88
	Nonrel.				0	1	3	12
%	Relational	82	84	89	84	82	48	80
	Nonrel.	18	16	11	16	18	52	20

trials or until it had gone through the sequence of six stimuli two times in a row without error. As a consequence *S*s averaged 48.8 training trials on these stimuli.

The *S*s' reactions to the 24 test stimuli are shown in Table 2. It should be noted that in 21 of these cases, the majority of *S*s chose the side predicted by the relational theory. The three exceptions are cases in which there is only one step difference in brightness between the top and bottom halves of the stimulus cards, i.e., stimuli 6/7, 5/6, and 4/5. Altogether, 80 per cent of the 264 test jumps are n keeping with a relational hypothesis. The extent of this accuracy can best be appreciated by noting that during this time *S*s were reacting to the three training stimuli per day with only 89 per cent accuracy despite all their previous training on these. Table 2 indicates that relational responding was least evident when the two grays differed by only one unit in brightness and for the darker grays, especially no. 7, which had the same reflectance value as the flat black paint used on the jumping stand.

The first statistical test made was to determine if there was any evidence of a progressive change in relational responding as the testing continued. Each *S* was tested on two stimuli each day, and a different pair of stimuli was used for each *S*. With the stimulus sets thus balanced from day to day, no evidence was found of a progressive change in the percentage of relational choices on test stimuli during this period nor of any change in the level of accuracy on the three training stimuli per day. Thus, while the continued training during the test period may have helped to maintain the tendency toward relational choices, there is no evidence that *S*s were actually learning such behavior during the test period.

In contrasting the predictions of a specific stimulus theory and a relational theory on these test stimuli, it is necessary to consider four different sets of test cards. On stimuli 1/2, 1/3, 2/3, 6/5, 7/5, and 7/6, both theories make the same prediction. For instance, on stimulus 1/2 the specific stimulus theory would predict a jump to the right because *S* had always been reinforced for jumping right in the presence of both these grays. Similarly, the relational theory would predict this because the top gray is lighter than the bottom one. On these six stimuli 94 per cent of the 66 test jumps were as predicted by both theories.

On the second set of stimuli, 2/1, 3/1, 3/2, 5/6, 5/7, and 6/7, the two theories make opposing predictions. For instance, on stimulus 2/1 the specific stimulus theory would predict a right jump because both grays had been associated with this response, whereas the relational theory would predict a left jump because the top gray is darker than the bottom one. On this set of six stimuli, 56 per cent of the responses were in the direction predicted by the relational theory; for six of the *S*s the majority of their jumps were relationally determined, for three of them their choices were split equally between the relational and specific directions, and for two the majority of their choices were in the direction predicted by the specific stimulus hypothesis. This percentage in favor of relational responding differs from a chance split between the .10 and .20 levels of significance. It should be noted that the majority of these test stimuli involve two grays that differ by only one step in brightness.

The third set of stimuli, 4/1, 4/2, 4/3, 4/5, 4/6, and 4/7, is that in which gray no. 4, which was always on the bottom half of the cards during training, is now on the top half. In terms of the specific stimulus theory this gray should be neutral, having been equally often associated with jumps to the right and to the left. Consequently, *S*'s response to these test stimuli should be entirely determined by the gray on the bottom half of the card. But this would always lead to just the opposite prediction from that of a relational theory, e.g., on 4/1 the specific stimulus hypothesis would predict a right jump because the gray no. 1 had been associated with this response, whereas the relational theory would predict a left jump because the top was darker than the bottom. On these stimuli 74 per cent of the jumps were relationally determined, which is well beyond the .01 level of significance.

The fourth and final set of stimuli, 2/5, 3/5, 3/6, 5/2, 5/3, and 6/3, is that in which one gray is lighter than the neutral gray no. 4 and the other is darker. On these the predictions from the specific stimulus theory are ambiguous. Presumably the response should be determined by two factors: (*a*) the gray on the top half of the card should have more influence than the one on the bottom because during training this one was always the determining cue, and (*b*) the gray of the pair that is farthest removed in brightness from the neutral gray no. 4 should have the greater influence because of generalization. Depending on how these two factors are weighted, a wide variety of predictions can be made. If only the top half of the card is considered, the predictions are exactly the same as for the relational theory. This latter theory makes unambiguous predictions for each stimulus in this set. For this set of stimuli, 95 per cent of the responses were in keeping with the relational prediction, a value significantly different from chance well beyond the .01 level.

If the 12 stimuli of sets 2 and 3 above, for which the two theories make opposing predictions, are combined, 65 per cent of the responses are in accordance with the relational hypothesis, a value significantly different from chance at the .01 level. If, as Table 2 suggests, part of the failure to show relational behavior on some of these stimuli is due to the difficulty of the discrimination when the two grays are separated by only one unit of brightness, a clearer picture of the predominance of relational responding is shown when this type of stimulus is excluded from the comparison. Considering the 6 stimuli in the above set of 12 in which the pair of grays differs by two or three brightness units, the percentage of relational responding increases to 80.

Five animals were given posttest training on a successive discrimination involving grays no. 3 and no. 5. During the original training these *S*s had shown the ability to discriminate between cards 3/4 and 5/4. If, as the specific stimulus theory seems to imply, gray no. 4 was neutral, then according to this theory *S*s must have been responding in terms of grays no. 3 and no. 5. Consequently, one would expect that they would continue to respond fairly accurately even though gray no. 4 was removed from the situation. Actually all discrimination between these two grays broke down, and there was little if any sign of learning during the 50 training trials. During the first 10 of these trials, *S*s chose correctly 50 per cent of the time, and during the last 10 trials they chose correctly 58 per cent of the time. This supports the idea that this discrimination is very difficult when *S*s must react to the stimuli as specific values, but that it is relatively easy when they can relate each of these grays to the reference gray no. 4 on a given trial.

DISCUSSION

In interpreting the results of this experiment, it should be borne in mind that the method of testing for transposition, and therefore the actual definition of the term transposition, in this study differs markedly from the usual method of testing. Usually *S* is presented during training with two stimuli and taught to approach one of these and avoid the other. Transposition is then tested by presenting *S* with two new stimuli. The implicit assumption is that the relationship between these new stimuli is the same as it was for the training pair. Thus, in this technique *S* always must select one of two simultaneously presented stimuli; in addition only the relationship, not the specific stimuli, remains constant from the training to the test situation.

In the present method the procedure is very different. While two stimuli are presented on each trial, *S* does not choose between them. Rather, *S* must react to the relationship between them by jumping either right or left. Again all the specific stimulus values that are used during the test situation have been used during the training situation; they are constant. The aspect of the situation that is varied from the training to the test trials is the relationship these specific stimuli bear to each other. The test for transposition is whether or not the behavior varies concomitantly with these changes in relationship. Because of these differences in procedure, it would seem likely that the present method should be a more sensitive test for relational responding than is the usual method. In a sense *S* is forced to respond relationally from the beginning of training. Furthermore, *S* is familiar with all the stimulus values used during the test so that these should not introduce any disruptive effect.

There would seem to be little question in terms of the present results that in most instances *S*s were reacting to brightness relationships rather than to specific brightness values. A relational hypothesis is able to make a specific, unambiguous prediction about each of the 24 test stimuli used. Eighty per cent of the test responses were in keeping with these predictions, a level of transposition that is almost as great as the level of accuracy these *S*s were able to maintain on the training stimuli during this period. Furthermore, it was shown that this level of accuracy was obtained on the very first day of testing and was not the result of learning or continued improvement during this period.

It is true that on the six test stimuli, 2/1, 3/1, 3/2, 5/6, 5/7, and 6/7, for which a relational hypothesis and a specific stimulus hypothesis make directly opposing predictions, only 56 per cent of the responses favor the relational predictions and 44 per cent the specific stimulus hypothesis. This small differential, however, is probably not representative of the true difference. It is especially questionable when it is noted that in the next set of test stimuli involving gray no. 4, where the two theories also make opposing predictions, the difference jumps to 74 per cent versus 26 per cent in favor of relational responding.

The lack of a significant differential in the first case seems to result from the difficulty of the discriminations involved in this set of tests. As can be seen from the logarithmic values for the reflectances in Table 1, the differences between grays no. 4 and no. 5 and between no. 6 and no. 7 are small as compared with the others. These two pairs of grays were the ones that gave results most opposed to the relational hypothesis, as shown in Table 2. This latter table also indicates two trends that lowered the percentage of relational responding. First, it indicates that when there was only one unit difference in brightness between the top and bottom half of a test stimulus, relational responding was reduced, suggesting that the grays employed were not spaced properly along the continuum for the most sensitive test of transposition. Secondly, it is evident that when the bottom half of a test card was gray no. 7, the darkest gray, relational responding was minimal. This gray has the same reflectance as the flat black used to paint the entire jumping stand. This suggests the possibility that as one of the grays on the card becomes very similar to the background gray, this similarity may dominate the response and mask the perception of the difference in brightness of the two grays on the card. In a sense the darker gray is amalgamated with the background so that relationship is obscured. If this hypothesis is correct, then this breakdown of relational responding on the dark grays should not have occurred if the background had consisted of stripes or some other distinct pattern.

Although the evidence from this experiment indicates that *S*s were responding to the relational aspects of the stimulus situation, this does not imply that this mode of responding is more basic or fundamental than responding to the absolute or particular characteristics of the situation. Certainly the evidence to date indicates that the particular aspects can be the determining factor in behavior in many situations. Rather, this study indicates that when these particular aspects are minimized as reliable cues for behavior in a given training situation, and the relational properties are emphasized, *S* is perfectly capable of responding to the latter.

It does suggest, also, that even in situations where *S* is presumably reacting to an absolute characteristic, behavior may be in part determined by the relation between this characteristic and the background stimuli. For instance in the usual successive discrimination involving black and white, this discrimination presumably would be easier to learn if the apparatus were painted a neutral gray than if it were either black or white. In the former case, the differential relations of "lighter than" and "darker than" between the two stimuli and the background should facilitate learning whereas these differential relationships would be lacking if the background was either white or black. The fact that these *S*s could discriminate the stimuli 3/4 and 5/4 during original training but were unable to discriminate between grays no. 3 and no. 5 during the posttest training supports this suggestion.

Acceptance of these results as evidence for the perception of, and response to, relationships suggests an alternative interpretation of those studies in which a correlation between mental age and amount of transposition behavior has been shown (1, 3). Usually these studies have been interpreted as evidence that the specific stimulus theories are correct, but that somehow the development of language responses permits more widespread transposition. The present study suggests this alternative. Children can respond relationally prior to the development of language, but do not necessarily do so in all situations. However, the very factors that lead to the development of language behavior also lead to an emphasis on relational responding as the dominant mode of behavior in the child. The result is a correlation between the rate at which language and relational responding develop.

The technique used in the present experiment should be equally applicable to studies of transposition phenomena involving size, form, or like dimensions. It would appear also to have advantages in the study of brightness thresholds. The rate of learning seems to be almost as great as on the usual simultaneous discrimination. At the same time much sharper contrasts between the two brightnesses can be obtained when both are on the same card than when they are spatially separated by the division between the two windows. Therefore, more sensitive measures of differential brightness thresholds should be obtained.

SUMMARY

Eleven albino rats were trained in a new type of transposition situation. The procedure consisted of training *S*s on a successive discrimination in which each stimulus card consisted of two grays, one brightness on the top half and a different one on the bottom half. When the top half was lighter than the bottom half, *S*s jumped to the right window, and when the top half was darker than the bottom half, they jumped to the left window. When this discrimination had been mastered, *S*s were tested on a set of 24 new relationships of this type. These were so selected that in 6 of them both a relational theory and a specific stimulus theory of transposition would make the same prediction, in 12 they would make opposing predictions, and in 6 the relational theory could make an unambiguous prediction whereas the specific stimulus theory could not.

1. For the entire set of 24 test stimuli, 80 per cent of the choices were as predicted by the relational theory.

2. For the set of six on which the two theories make the same prediction, 94 per cent of the choices were in agreement with them.

3. For the set of 12 on which the two theories make opposing predictions, 65 per cent of the choices were as predicted by the relational theory.

4. For the set of six on which only the relational theory could make an unambiguous prediction, 95 per cent of the choices were in this direction.

5. It is suggested that this technique should prove valuable in the study of other forms of transposition behavior and in the study of differential brightness thresholds.

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Received March 5, 1954.

MULTIPLE DISCRIMINATION LEARNING BY WHITE RATS

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In an earlier study (1), 80 different stimulus cards were presented in more than 240 separate combinations to 11 white rats. Although these rats had eventually learned to respond in quick succession to many different positive stimuli, it was assumed that the basis of these earlier discriminations was the presence of a common logical element in all the positive cards, i.e., the quality of "triangularity." No one has repeated this work with nonrelated stimuli, and no serious attempt has been made to find out how many diverse visual discriminations a particular rat can learn and remember simultaneously. It was our purpose to investigate this problem as a first step in a study of the length of the discrimination series best suited to reveal learning decrements resulting from exposure to certain potentially harmful stimuli.

METHOD

Subjects

Twenty adult male albino rats of the Sprague-Dawley strain were selected at random from the larger group in the laboratory colony. They were approximately nine months old and weighed 380 gm. (average) at the start of the experiment. Their weight was reduced to 309 gm. during orientation to the problem before actual training to the pairs of cards was started, after which the weight was allowed to increase slowly. These rats were tested over a seven-month interval.

Apparatus

Three single units of the multiple visual discrimination apparatus (2) previously described were used.

A large number of stimulus cards was assembled in dissimilar looking pairs. These pairs were then arranged in a series, so that, in *Es'* judgment, the rat would not be rewarded with food by responding consistently to any single stimulus variable. Retinal extension, brightness, reflectance, total area, shape, pattern, and position of the object on the card were all varied in the series.

The pairs of stimulus cards used are shown in Figure 1. The columns are numbered from top to bottom, and cards occupying the same relative position in two adjacent columns constitute one pair. Thus, in Experiment I, cards 1 and 6 through 5 and 10 make up the first series, cards 11 and 16 start series II, cards 41 and 46 start series III, and cards 51 and 56 start series IV. Additional stimuli are shown in Figure 2.

Procedure

The positive stimulus card was randomly shown in all five apertures of the multiple discrimination apparatus. Each stimulus was exposed in adjacent apertures while the other three contained plain black cards. The positive card of each pair was randomly determined before training was started, and the negative card was always locked. The rat was rewarded immediately after each jump to the positive card, and was required to correct its errors. Each card of a pair was the positive stimulus for half the animals in Experiment I.

The right-left position of the positive card and the pair of apertures used were determined from tables of random numbers and latin squares. The side on which the animal was introduced to the jumping platform was also randomized. No rat was run on two successive days by the same *E*. Although three separate discrimination units were used simultaneously, except for test trials and photographic purposes the training given a particular rat was on the same platform. After the rats had developed speed on the problem, ten successive trials were given in the morning and ten in the afternoon.

Because of uncertainty concerning the rat's ability to memorize a large number of different stimulus cards, Experiments I and II were run concurrently. The rats in Experiment I (modified whole method) were required to learn five pairs presented in strict serial order to a criterion of 15 consecutive correct jumps to three successive repetitions of the same five pairs, while the rats in Experiment II (part method) learned each pair to a criterion of 10 consecutive correct jumps before going on to the next pair.

Preliminary training. Of the rats to be used on the five-pair problem of Experiment I, seven were trained to jump to a single vertical 20-mm. stripe and seven to a single horizontal 20-mm. stripe when presented with four black cards in the other apertures of the discrimination unit. After they were jumping rapidly, 20-mm. striae were substituted for the single stripe. There was a complete and immediate positive transfer. Then a second card with striae was introduced so that the rats had to choose between the appropriate vertical

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[1] This paper contains nonclassified data from Project No. 21-3501-0003 collected while the author was at the USAF School of Aviation Medicine. It was presented before the Southern Society for Philosophy and Psychology at Austin, Texas, April 1953. The opinions expressed herein are the author's and not necessarily those of the Department of the Air Force.

The author is indebted to Richard S. Massar, Robert B. Feldscher, Hugh L. Perry, Richard E. Nye, Dale L. Ott, Charles A. Shaw, and Dr. George T. Hauty for assistance in many phases of the study.

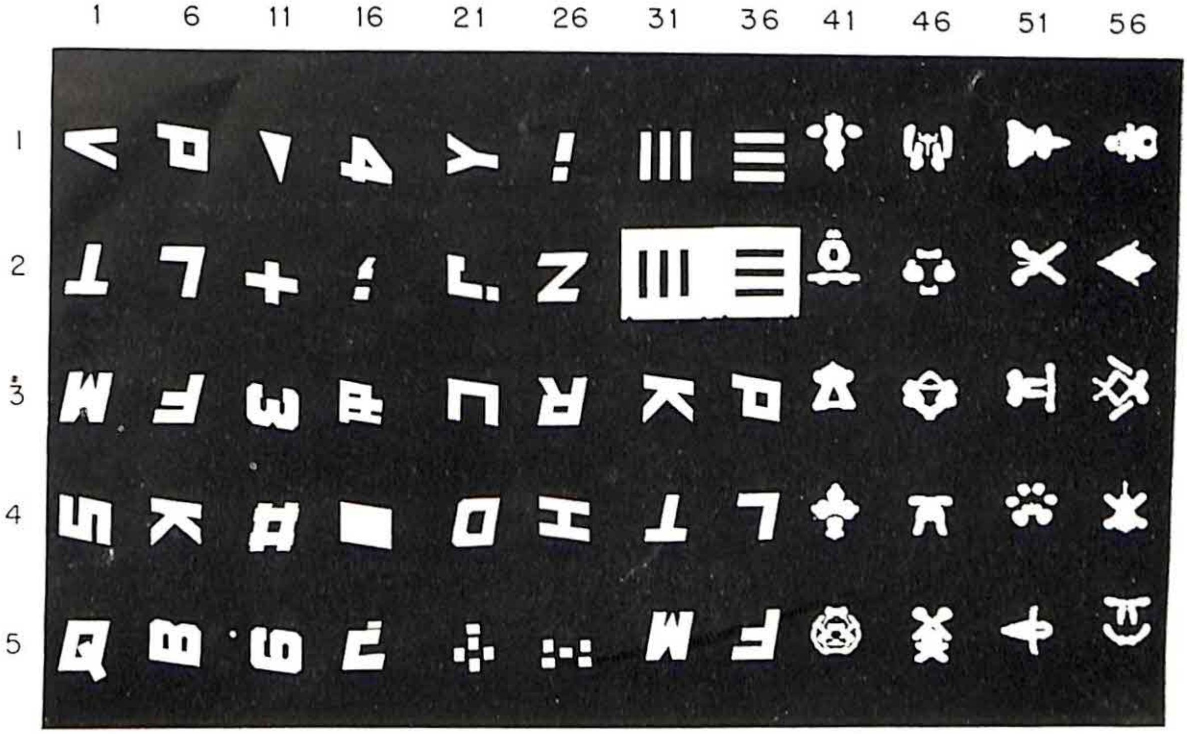

FIG. 1. Designs used on stimulus cards

and horizontal 20-mm. striae. On successive days the width of the striae was reduced through 15, 10, 7.5, and 5 mm., and only those animals were retained which successfully discriminated the smallest striae without further training. Only one rat (trained to vertical as positive) failed at the 5-mm. level. It was assumed that in addition to providing a rough check on the individual rat's acuity, this habit of "looking for differences" which was necessary to a successful solution of the acuity problem might possibly transfer when the perceptual symbols of the main experiment were introduced.

RESULTS

Experiment I

Table 1 presents the performance data for all rats on each of four successive series of five pairs of cards. One rat failed to meet the criterion on series I and two failed on series II. Guided training (2, p. 71) consisting of presentation of each of the five positive cards in serial[1] order with four black cards was given at the start of series III, for a total of 45 jumps. After this all rats successfully met the criterion in 136 jumps (28 repetitions of the series). All rats were then retested on the previous 15 pairs of cards in quick succession, and six rats met the .01 level of confidence on the first test trial. They were next trained under greatly increased illumination so that motion picture records of their discriminative behavior could be obtained.[2]

These records show rats trained on the serial problem making 15 consecutive correct jumps to these 15 pairs. The rats were able to maintain the discrimination above the .01 level of confidence the first time the order in which the pairs were presented was randomized. This indicated that the response was not dependent upon the serial order of presentation. Next a positive card was exposed with a negative card from some other previously learned pair, and the accuracy remained unchanged. The next step involved randomization of the order of presentation of the positive cards and presentation of them with a familiar negative card from another pair in a single 15-pair series. Three rats tested on this problem maintained their accuracy above the .01 level on the first test trial after both of these changes had been made, and also after the familiar positive cards were presented with completely strange patterns as the other

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[2] Nonclassified personal motion pictures of these rats performing on various discrimination tests were shown at the 1952 meeting of the American Psychological Association and the 1953 meeting of the Southern Society for Philosophy and Psychology.

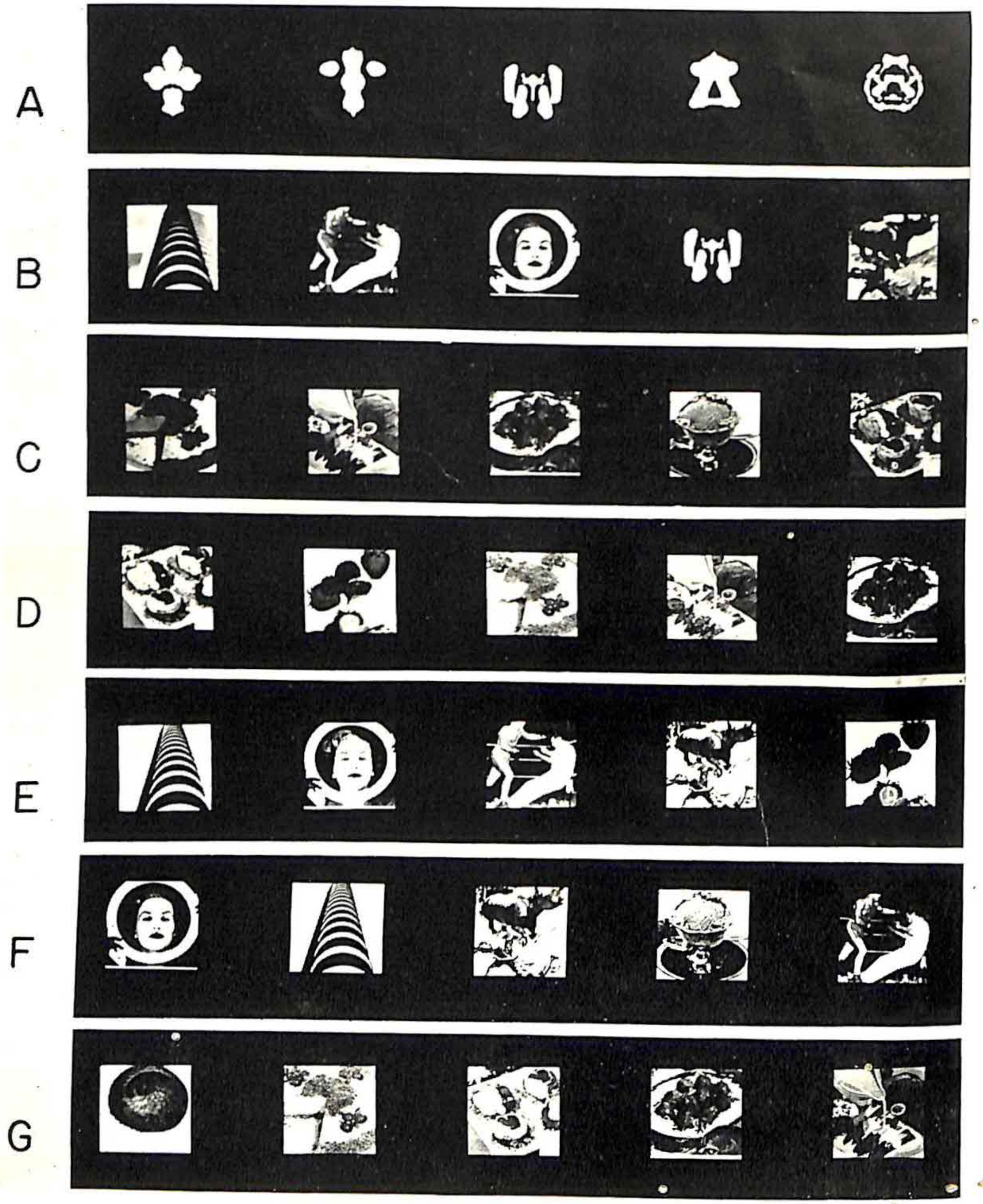

FIG. 2. Examples of multiple stimulus settings

member of the pair. One rat was photographed while being given 5 guided trials to an advertisement. When this advertisement was presented with a second, it was chosen on 9 of the first 10 jumps. When the same advertisement was presented in a panel of 5 dissimilar advertisements, it was immediately chosen 20 consecutive times.

Because of the break in training during the photographing of the rats on these new test problems and the loss of some of our experimental personnel, the six slowest rats

TABLE 1

Number of Jumps per Five-Pair Series before Making 15 Consecutive Correct Jumps

Series No.	Cards	Rats Meeting Criterion	Average Trials	Range	Guided Jumps
I	1–6	12/13	210	70–388	0
II	11–16	11/13	149	96–196	0
III	41–46	13/13	83	0–136	45
IV	51–56	7/7	92	35–249	50

were eliminated. The seven remaining rats all met the criterion to the new cards in series IV. All of these were tested on 20 pairs of cards in quick succession in a single-trial period for six consecutive days. Every rat was above 80 per cent accuracy for the entire period, and three met the criterion of 18 correct unaided discriminations out of 20 jumps on the first day.

After the rats had completed the retest on the 20 pairs in a single series, the two that were again tested on new combinations of old positive and negative cards in a randomized order had no loss in accuracy. Attempts to get these experienced rats to pick one picture when presented with four new pictures after only one guided trial to the positive card failed, although it was done with as few as three trials. The 20 pictures used in this part of the study were all new to the rats (advertisements cut from magazines, as in Fig. 2).

Experiment II

The data for the six rats that had been assigned the problem of learning each pair to a criterion before going on to the next pair are presented in Table 2. These rats had originally been trained to jump to the vertical stripe, and were all required to jump to the smallest numbered card (left-hand one) of each pair (see Fig. 1).

It will be noted that the problems varied in difficulty and that the same problem also varied in level of difficulty for individual rats. Thus, they may not have been responding to the same cues from the stimulus cards.

TABLE 2

Number of Jumps per Pair before Making 10 Consecutive Correct Jumps

Problem No.	Cards	Rats Meeting Criterion	Average Trials	Range
1	11–16	6/6	8	3–10
2	12–17	6/6	35	13–51
3	13–18	6/6	59	34–73
4	14–19	6/6	17	0–44
5	15–20	6/6	17	1–44
6	21–26	6/6	12	2–21
7	22–27	6/6	7	0–19
8	23–28	6/6	27	1–62
9	24–29	6/6	34	2–70
10	*	6/6	74	2–136
11	†	4/6	135	81–206
12	5–10	5/5	73	25–191
13	25–30	5/5	24	0–61
14	31–36	5/5	2	0–9
15	‡	4/4	24	20–34
16	33–38	4/4	45	20–68
17	34–39	4/4	13	3–33
18	35–40	4/4	24	18–31

* E-A rotated 180°.

† Circle-square with area of 12.25 sq. in.

‡ Upright and inverted U.

Because of the rapidity with which they learned the first nine problems, these rats were tried on some discriminations which had proven difficult for others. Problems 10, 12, and 15 were difficult probably because of confusion with other cards in the series, but were eventually learned by all rats. Two of the six rats failed problem 11 (circle-square), probably because of acuity requirements of the stimuli, as pointed out by Lashley (4). After the four quickest-jumping rats had learned 18 pairs, they were retrained to the 15 pairs shown in Figure 1 in a consecutive series, starting with cards 11 and 16 and ending with cards 35 and 40. The four most difficult of the original 18 pairs had been eliminated (problems 10, 11, 12, and 15) and a new problem (cards 32 and 37) added. This latter problem was of interest because of the brightness reversal involved. All the rats met the .01 level of confidence on the second day of the retest.

DISCUSSION

No formal experiments have been conducted to compare the effects of guided versus conventional discrimination training. Additional supplementary data were secured after completion of a later series of unpublished experiments where 12 young control rats had learned four different series of five pairs of cards. Each rat was then able to meet the .01 confidence level in its first discrimination test run after having been given only ten previous guided trials. The speed and certainty with which each of these 12 rats picked the one advertisement (a different one for every rat) from a panel of five was very impressive.

Since this apparatus and method evidently "put the questions in a way that was intelligible even to rats" (5, p. 28), some question has arisen as to whether or not the rat's newly demonstrated capacities should rate it a higher position in the evolutionary scale of intelligence. Lashley has emphasized that "the limits of capacity of each order of animals are set by the kinds of relations among objects that it can perceive" (5, p. 31). In this study, an attempt was made to minimize the possibility of discriminations based on a perception of broad relationships and to force the rat to remember a great variety of minute visual details. The lack of similar studies prohibits interspecies comparisons at this time. However, the speed with which a large number of diverse visual discriminations has been learned and simultaneously remembered would seem to qualify the white rat as a useful *S* for preliminary investigations of the effects of various harmful stimuli upon complex psychological processes. The short life span of the rat makes it especially valuable for experiments in which *S* is exposed to some experimental variable at an early age and the effects studied as it grows older (3) or over successive generations.

SUMMARY AND CONCLUSIONS

Nineteen male albino rats were trained to discriminate between paired visual stimuli on the multiple visual discrimination apparatus. For 13 of the animals a modified whole method was used, where the cards were always presented in rigid series of five pairs each, and for six rats a strict part method was used. So long as cards in a stimulus series did not closely resemble cards which had called for the opposite response in an earlier series, and were easily within *S*'s limits of acuity, these white rats were able to learn and to retain a discrimination series of considerable length. Fifteen- and twenty-pair series learned by the part and the modified whole method do not represent the upper limits of the rat's ability.

Some insight into the nature of the rat's response to the positive card is revealed by the fact that 20 pairs composed of 40 unique cards which had been learned in rigid serial order in five-pair series were responded to perfectly after (*a*) the order of the pairs was randomized, (*b*) each of the 20 familiar positive cards was randomly paired with 20 familiar negative cards, (*c*) the positive card was paired with new strange cards, (*d*) all three of the above were combined in one continuous series of 25 consecutive pairs at a single trial.

After previous training to many paired stimuli, rats were able, in as few as five (and in some cases, three) guided trials to a single card, to pick the one new advertisement from a panel of five at better than the .01 level of confidence on their first ten discrimination runs. Such rapid learning is difficult to explain on the basis of the limited perceptual ability conceded to the rat heretofore.

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Received June 4, 1953.